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Influence of zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis*) mussel invasions on benthic nutrient and oxygen dynamics

Caroline B. Turner

Abstract: Although invasive zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis*) mussels are known to increase water column concentrations of nitrogen and phosphorus, the relative roles of direct nutrient release by the mussels and mussel-induced alterations to sediment fluxes are little understood. In short-term microcosm experiments comparing the presence and absence of mussels on sediments from Oneida Lake, New York, USA, both dreissenid species approximately doubled benthic oxygen consumption and fluxes of ammonium. The impact on soluble reactive phosphate (SRP) flux varied from 40% to 140% depending on whether mussels were located in the water column or directly on sediments. The additional flux was attributable directly to release by the mussels, with fluxes from the sediments remaining largely unchanged. However, mussels located directly on sediment surfaces released twice as much SRP as mussels located higher in the water column, with a molar N:P ratio as low as 4:1. The high rate of SRP release by mussels on sediment, possibly caused by mobilization of iron-bound phosphorus from sediment particles in the anoxic guts of the mussels, could contribute to observed increases in SRP, abundance of nuisance algae such as *Cladophora*, and abundance and toxicity of the cyanobacteria *Microcystis* in dreissenid invaded ecosystems.

Résumé : Bien qu'on sache que les moules zébrées (*Dreissena polymorpha*) et les moules quaggas (*Dreissena rostriformis*) envahissantes accroissent les concentrations d'azote et de phosphore dans la colonne d'eau, on connaît mal les rôles relatifs de la libération directe des nutriments par les moules et des modification des flux dans les sédiments induites par les moules. Lors d'expériences de courte durée dans des microcosmes de comparaison de la présence et de l'absence des moules dans les sédiments du lac Oneida, New York, É.-U., les deux espèces de dreissenidés ont augmenté par un facteur d'environ deux la consommation benthique d'oxygène et les flux d'ammonium. L'impact sur le flux de phosphate réactif soluble (SRP) variait de 40 % à 140 % selon que les moules étaient situées dans la colonne d'eau ou directement sur les sédiments. Le flux additionnel est attribuable à la libération directe par les moules, car les flux en provenance des sédiments sont demeurés en grande partie inchangés. Cependant, les moules sises directement à la surface des sédiments libèrent deux fois plus de SRP que les moules situées plus haut dans la colonne d'eau, avec un rapport N:P molaire aussi faible que 4:1. Le taux élevé de libération de SRP par les moules sur les sédiments, causé peut-être par la mobilisation de phosphore lié au fer à partir des particules de sédiments dans les tubes digestifs anoxiques des moules, pourrait contribuer aux augmentations observées de SRP, à l'abondance des algues nocives telles que *Cladophora* et à l'abondance et la toxicité des cyanobactéries *Microcystis* dans les écosystèmes envahis par les dreissenidés.

[Traduit par la Rédaction]

Introduction

The invasion of zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis*) mussels has dramatically altered freshwater ecosystems in North America. Because the mussels are benthic filter feeders and grow to high densities, they have shifted ecosystem resources from pelagic to benthic and littoral zones of lakes (Hecky et al. 2004; Zhu et al. 2006). Not only have phytoplankton and zooplankton abundances declined (Strayer et al. 1999; Vanderploeg et al. 2002), but inorganic nutrient availability has changed as well. Substantially higher after-invasion concentrations of soluble reactive phosphorus (SRP) have been measured in lakes (Makarewicz et al. 2000; Conroy et al. 2005*b*; Upstate Freshwater Institute 2006) and rivers (Caraco et al. 1997; Effler et al. 2004). Ammonium and nitrate concentrations have also increased in many systems (Johengen et al. 1995; Effler et al. 1996; Makarewicz et al. 2000), and oxygen concentrations have declined (Effler et al. 1996; Caraco et al. 2000; Schloesser et al. 2005).

These changes in nutrient availability have important implications for aquatic ecosystems, favoring the growth of *Cladophora*, a nuisance filamentous alga (Hecky et al. 2004; Higgins et al. 2008), and *Microcystis*, a cyanobacterium with toxic strains that can threaten public health and deter zooplankton grazing (Vanderploeg et al. 2001; Raikow et al. 2004; Conroy et al. 2005*b*). Increased SRP in the water column promotes increased abundance of *Microcystis* (Bierman et al. 2005). Although not all *Microcystis* are

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toxic, concentrations of the microcystin toxin are also higher in many lakes invaded by dreissenids (Knoll et al. 2008).

While many studies have documented the correlation between the invasion of dreissenid mussels and increases in inorganic nutrients, the mechanism of this increase is not well understood. The source of additional inorganic nutrients may be either consumption of phytoplankton and release of nutrients by the mussels or altered microbial nutrient cycling in the sediments. Determining the relative contributions of these sources has implications for the long-term nutrient trends in invaded lakes. Because sediments contain large nutrient pools and sediment processes operate over long time scales (Schlesinger 1997), alteration to sediment nutrient cycling could lead to larger and longer-term increases in water column nutrient availability than changes in phytoplankton dynamics alone.

Direct excretion of ammonium and phosphate by dreissenid mussels is one potential mechanism of increased nutrient availability. While strictly speaking not all nutrient release by mussels is excretion, I use the term excretion throughout to refer to any release of dissolved inorganic nutrients by the mussels. Arnott and Vanni (1996) calculated that excretion of phosphate by zebra mussels constituted a substantial portion of the benthic phosphorus flux in Lake Erie. In addition to the absolute amounts of nutrient released, mussel excreta have a low N:P ratio, which could shift the phytoplankton community toward cyanobacteria (Arnott and Vanni 1996). These excreted nutrients could be derived solely from phytoplankton previously consumed by the mussels. However, it is also possible that a portion of the phosphorus released by mussels was previously bound to oxidized iron in ingested particles. Because mussels' guts are anoxic, ingested iron may be altered to reduced, soluble form, thus releasing any associated phosphorus (Hecky et al. 2004).

In addition to direct excretion, several studies have found that mussels can also influence the rate of nutrient release from sediments. Increased nitrification and denitrification rates (Bruesewitz et al. 2006, 2008), increased nitrate uptake, and decreased phosphorus uptake (Bykova et al. 2006) were observed in sediments underlying zebra mussel colonies. Mussels could also increase sediment oxygen consumption via deposition and decomposition of organic matter in feces and pseudofeces (composed of particles that were ingested but not digested). Increased oxygen consumption would, by altering oxygen availability, affect many other sediment nutrient processes. In addition to the effects of living mussels, both dreissenid species produce empty shells, which accumulate on the sediment surface (Strayer and Malcom 2007) and could potentially act as a barrier to diffusion at the sediment–water interface.

Another important question is whether zebra and quagga mussels have differing impacts on nutrient cycling. Zebra mussels grow to high densities on hard substrates (Mellina and Rasmussen 1994), but can also colonize soft substrates (Berkman et al. 1998). Quagga mussels preferentially colonize soft substrates and occur at greater depths than zebra mussels (Mills et al. 1996), although in some lakes, quagga mussels are now more abundant than zebra mussels even in shallower habitats and on hard substrates (Wilson et al. 2006). Differences in habitat use between zebra and quagga mussels could affect their impact on benthic nutrient and oxygen dynamics, but this has not been studied. Previous studies of effects on sediment nutrient processing have focused solely on zebra mussels (e.g., Bruesewitz et al. 2006; Bykova et al. 2006); thus, the role of quagga mussels in these processes is unknown. If the two species differ in their impact, that would indicate that systems already invaded by one species face further alteration in the event of subsequent invasion by the other species.

To evaluate the impact of zebra and quagga mussels on benthic fluxes of ammonium, nitrate, SRP, and oxygen, I completed a set of microcosm experiments using water and sediments from Oneida Lake, New York, USA. These experiments were designed to compare the magnitude of fluxes from mussel excretion with the magnitude of alterations to sediment fluxes caused by the mussels. Since zebra mussels can inhabit both soft and hard substrates, I compared the benthic fluxes associated with zebra mussels located directly on the sediments with those of zebra mussels located above the sediments. I also compared fluxes associated with zebra and quagga mussels located directly on the sediments. In addition, I measured the impact of empty zebra mussel shell accumulation on benthic fluxes.

Materials and methods

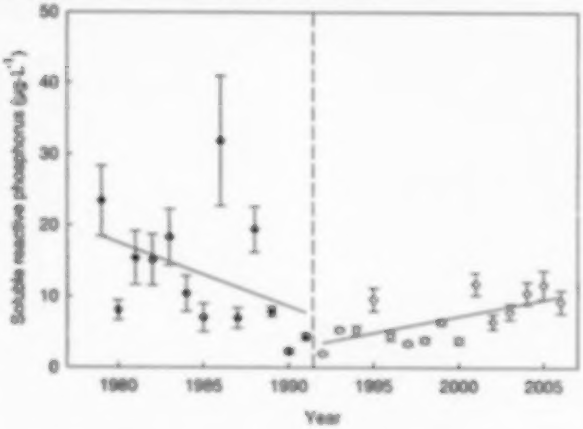
Site description

Oneida Lake is a shallow, polymictic, eutrophic lake in upstate New York. It has an average depth of 6.8 m and a surface area of 206.7 km^2 (Mills et al. 1978). Zebra mussels were first observed in the lake in 1991 and in 1997 reached mean densities of 45 000 $mussels{\cdot}m^{-2}$ on hard substrates and 3000 $mussels{\cdot}m^{-2}$ on soft substrates (Mayer et al. 2002). While variable from year to year, mussel densities have not exhibited an overall trend of increase or decrease in the lake (Rudstam and Mills 2008*a*). No quagga mussels had been observed in Oneida Lake at the time of this experiment (2007); however, quagga mussels were observed in most samples throughout the lake the following year (E.L. Mills, Cornell Biological Field Station, 900 Shackelton Point Road, Bridgeport, NY 13030, USA, personal communication, 2009). In the years since the invasion of zebra mussels, SRP concentrations in the lake have steadily increased (Fig. 1).

Experimental design

To test the role of mussels and their interaction with sediments in affecting benthic fluxes, I carried out microcosm experiments using both zebra and quagga mussels. The five treatments ($n = 5$) in the experiment consisted of a mussel-free control, quagga mussels on sediments (Q-sediment), zebra mussels on sediments (Z-sediment), zebra mussels suspended in a loose plastic mesh in the water column 3 cm above the sediments (Z-water column), and empty zebra mussel shells on the sediments (shell). The inclusion of both the Z-sediment and Z-water column treatments allowed me to compare the impact on sediment nutrient flux of mussels living directly on the sediments with the impact of mussels attached to rocks or macrophytes, which influence the sediments only through deposition. The shell treatment simulated the effect of accumulated mussel shells on sediment processes. The replicates were arranged in a randomized

Fig. 1. Long-term trends in annual mean (± standard error) concentration of soluble reactive phosphorus (SRP) in Oneida Lake. Means are averages of weekly samplings (June–September) at five sampling stations throughout the lake. The dashed line indicates date of zebra mussel invasion. Linear regressions are shown for before-invasion (1979–1991, solid diamonds) and after-invasion (1992–2006, open diamonds) years. There is no significant trend before-invasion (least squares linear regression, $r^2 = 0.09$, $p = 0.17$). After-invasion SRP concentration increases significantly over time (least squares linear regression, $r^2 = 0.40$, $p = 0.007$). Raw data taken from Rudstam and Mills (2008*b*).



complete block design to account for variation in position in a continuous inflow water tank.

I measured flux rates of oxygen, nitrate+nitrite, ammonium, and SRP in each core. For all cores containing live mussels (Z-water column, Z-sediment, and Q-sediment), I measured flux rates both with and without mussels present. By subtracting the flux without mussels from the flux in the presence of mussels, I was able to calculate the excretion rates of the mussels.

Microcosm setup

For microcosm sediments, I used a mixture of sand and mud collected at a depth of 1 m about 5 m from the shore of Oneida Lake. No live zebra mussels were present in these sediments, likely because of annual removal by ice scour. Sediments were sieved using a 500 µm sieve and homogenized prior to use in experimental cores.

I collected zebra mussels from rocks in Oneida Lake, using a razor blade to cut byssal threads. Quagga mussels were collected from Cayuga Lake, New York, from soft sediments at a depth of 25 m using a Ponar dredge. All zebra and quagga mussels used for the experiment had shell lengths of 10–15 mm, the most abundant size class of zebra mussels collected in Oneida Lake. For both species, all individuals in a given area were collected and selection of individuals for inclusion in microcosms was based solely on size. I scrubbed all shells using a toothbrush to remove sediment and attached algae. For the shell treatment, I also removed mussel tissue from the shells. While the scrubbing of shells may not have removed all associated organic matter, this method was used for consistency with the live mussel treatments.

Experimental cores consisted of 9.5 cm diameter × 32 cm tall polycarbonate cylinders, sealed at the base with a rubber stopper. I added 15 cm of sediments to each core. The cores equilibrated for 2 weeks, submerged in a freshwater tank with a continual inflow from Oneida Lake. The turnover time of water in the tank, assuming perfect mixing, was approximately 1 h; however, because of reduced mixing, turnover time was likely longer in the cores themselves. When submerged, each core contained 1.1 ± 0.1 L of water. This tank was located in a temperature controlled experimental chamber at the Cornell Biological Field Station, Bridgeport, New York. Water temperature averaged 17 °C. Cores were maintained in the dark (simulating light-free conditions at the bottom of a eutrophic lake), and each core was individually aerated using an air stone. The aeration also ensured a continual movement of water into and out of each core.

I added mussels to the treatments at the end of the 2-week equilibration period while keeping experimental conditions otherwise constant. I added 20 organisms to each noncontrol core, for a density of 2800 mussels·m^{-2}. This is similar to the average density of 3000 mussels·m^{-2} for soft sediments in Oneida Lake in 1997 and much lower than the densities observed in rocky habitat (Zhu et al. 2006). To maintain treatments with mussels living directly on the sediments, I returned any mussels attached to core walls back to the sediment surface at least daily during the experiment. I measured the combined wet mass with shell for the 20 mussels and individual mussel length at the beginning and end of the 21-day experiment. The total initial wet mass (including shells) of the zebra mussels added to each core was 6 ± 0.1 g. Because of differences in morphometry between the species, the initial wet mass with shell for quagga mussels was 3 ± 0.1 g per core.

Oxygen and nutrient flux measurements

I measured the rate of dissolved oxygen (DO) consumption in each microcosm on days 7, 14, and 21. To do so, I placed a sealed polycarbonate lid with a sampling port over each core, siphoned off the overlying water in the core, and replaced it with water pumped from Oneida Lake. Care was taken to ensure that sediments were not disturbed and that no air bubbles were present. A magnetic stir bar maintained well-mixed conditions in the water column of each core without disturbing the underlying sediments. All incubations were completed in the dark. I fit a self-stirring YSI DO probe (model YSI 5905; calibrated on each day of use) snugly into the sampling port. On days 7 and 14, I allowed oxygen readings to stabilize for 3 min and then recorded oxygen concentration at 3 min intervals for a total of 30 min. On days 7 and 14, I did not remove mussels from the sediments to avoid disrupting the sediments midway through the experimental period. As a result, there are no flux values for the Z-sediment and Q-sediment treatments on those dates. On day 21, I measured oxygen concentrations hourly for 4 h in conjunction with nutrient sampling, as described below.

On day 21 of the experiment, I measured benthic nutrient flux, the rate of production or consumption of a given nutrient by sediments and mussels (where present) in each core. At the start of each flux measurement, I refilled, sealed, and stirred the cores as described for oxygen flux measurements above. I collected 40 mL water samples hourly from each core for 4 h and measured DO and temperature at the time of each collection. I replaced the removed volume of lake water with fresh water pumped from Oneida Lake. Upon collection, I filtered all water samples using a 0.45 μm Supor polyethersulfone filter and froze the filtrate for later analysis. The flux rates for cores with live mussels present were measured first. I then removed the mussels using forceps, taking care not to disturb the sediments. I drained the overlying water from these cores and refilled them with fresh Oneida Lake water before measuring flux rates in the absence of mussels. To account for any changes in concentration that were due to water column rather than sediment processes, I also measured rates of change in concentration in a water-only core containing neither sediments nor mussels.

I analyzed ammonium, nitrate+nitrite, and SRP concentrations of collected water samples on a Lachat Instruments QuickChem 8000 autoanalyzer. I then used these measurements to calculate rates of nutrient flux ($mg \cdot m^{-2} \cdot h^{-1}$).

Calculations and statistics

I calculated the flux rate in each core for each chemical species as the average change in concentration of that chemical per unit area over the five time points (see Fig. 2 for sample graph and calculation). To exclude the consumption or production of nutrients or oxygen in the water column, I subtracted the volume-corrected flux of the chemical species of interest in water-only cores from the flux in each core. This was typically a correction of less than 30% for DO and nitrate+nitrite and less than 10% for ammonium and SRP.

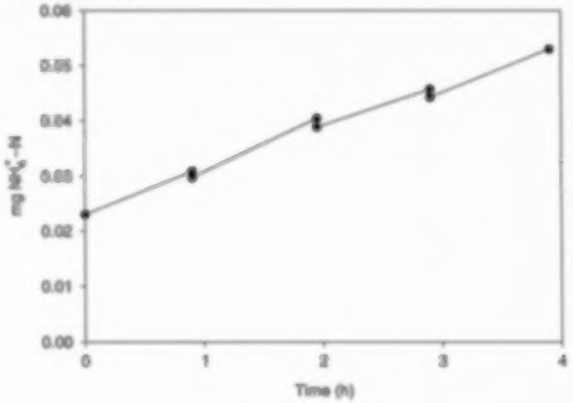
Excretion rates of ammonium and SRP by the mussels were calculated by subtracting the flux rate in sediment-only cores from the flux rate of mussel + sediment cores. For example, to calculate the phosphate excretion by mussels in a particular core, the rate of phosphate flux in the core after the mussels were removed was subtracted from the phosphate flux in that same core with the mussels present.

To determine whether the five treatments (control, Z-water column, Z-sediment, Q-sediment, and shell) affected sediment nutrient and oxygen fluxes, I calculated analyses of variance (ANOVAs) for the rates of nutrient and oxygen flux in sediments without live mussels. Similarly, to determine whether there was a difference in excretion by mussels in the three treatments with live mussels (Z-water column, Z-sediment, and Q-sediment), I calculated ANOVAs for mussel excretion of nutrients and consumption of oxygen. For all ANOVAs, both treatment and block were included as independent variables. I determined post hoc differences among treatments using Tukey's test with a cutoff value of $p < 0.05$. I also used *t* tests to determine whether mussel excretion of nutrients differed significantly from zero. All statistical analysis was completed using JMP 8 statistical software (SAS Institute Inc., Cary, North Carolina).

Estimation of nutrient release due to respiration

Based on the rate of oxygen consumption by mussels, I calculated rough estimates of N and P release from mussels that could be attributed to consumption and subsequent respiration of organic matter. For the purposes of this calculation, I assumed that (*i*) respiration accounts for all oxygen consumed by the mussels, (*ii*) organic matter filtered from the water column and respired by the mussels has the Redfield C:N:P molar ratio of 106:16:1 (Redfield 1958), and (*iii*) all N and P in respired organic matter is excreted rather than assimilated by the mussels. The C:N:P ratio of phytoplankton is known to vary widely in lakes (Downing and McCauley 1992), but for most lakes C:N and C:P are higher than the Redfield ratio (Hecky et al. 1993; Elser et al. 2000); therefore, the assumption of the Redfield ratio likely provides an upper end estimate of the of the amount of N and P released through respiration. Similarly, the first and third assumptions, while almost certainly not strictly accurate, provide an upper-limit estimate of the amount of nutrient release that could be explained by metabolic activity.

Fig. 2. Example graph showing the change in the mass of ammonium in the water column over a 4 h period for one core. The mass was calculated by multiplying the concentration of ammonium by the volume of water in the core. Lines are not continuous because of the removal of water for nutrient analysis at each time point and replacement of that water with fresh lake water. To calculate the flux of ammonium ($mg\ NH_4^+ \text{-} N \cdot m^{-2} \cdot h^{-1}$), the average slope of the four lines was divided by the surface area of sediment in the core. These calculations were repeated for all 25 cores and for all flux species (ammonium, nitrate+nitrite, soluble reactive phosphate (SRP), and oxygen).



To calculate the amount of N and P that could be released through respiration, I first calculated the average number of moles of O_2 consumed by mussels in a given treatment. Since respiration involves the consumption of one atom of C for every molecule of O_2, this is equivalent to the moles of C consumed. I then calculated associated N and P release using the Redfield ratio.

Results

Mussel growth

The zebra and quagga mussels were observed to be actively filtering throughout the experiment. Only one zebra mussel and no quagga mussels died during the 21 days. In all but one of the cores with live zebra or quagga mussels, there was a net increase in mass and average length of the mussels. Mass increase in these cores ranged from 5% to

Table 1. Summary of two-way analysis of variance (ANOVA) results for all nutrient and oxygen flux measurements.

			Overall		Block		Treatment	
Flux type	Source	df	*F*	*p*	*F*	*p*	*F*	*p*
DO (day 7)	Sediment	8	2.267	0.141	0.515	0.727	**5.769**	**0.028**
DO (day 14)	Sediment	8	**3.689**	**0.046**	**4.630**	**0.031**	1.807	0.225
DO (day 21)	Sediment	16	**6.025**	**0.001**	**6.294**	**0.003**	**5.756**	**0.005**
	Mussels	8	**7.423**	**0.006**	**10.986**	**0.003**	0.297	0.751
NH_4^+	Sediment	16	**6.865**	**<0.001**	**10.056**	**<0.001**	**3.674**	**0.026**
	Mussels	6	**5.506**	**0.029**	**5.758**	**0.030**	2.634	0.151
SRP	Sediment	16	2.406	0.064	**4.132**	**0.017**	0.680	0.616
	Mussels	6	**6.440**	**0.020**	2.796	0.126	**15.541**	**0.004**
$NO_3^- + NO_2^-$	Sediment	16	1.989	0.115	**3.221**	**0.041**	0.757	0.568
	Mussels	6	2.536	0.141	3.780	0.072	0.586	0.585

Note: Significant effects ($p < 0.05$) are indicated in bold. DO, dissolved oxygen; SRP, soluble reactive phosphate.

30% and length increased by 2%–12%. Both mass (df = 7, $F = 92.7$, $p < 0.0001$) and length (df = 8, $F = 54.7$, $p = 0.0001$) increase varied significantly by treatment. Quagga mussels showed a significantly greater increase in length and mass than zebra mussels, but there was no significant difference in growth between zebra mussels on the sediments and those suspended in the water column (Tukey's test, $p < 0.05$).

Oxygen consumption

DO declined over time in all flux measurements in all cores, indicating a net consumption of oxygen by both sediments and mussels. On days 7 and 21, sediment oxygen flux differed significantly among treatments (Table 1, Figs. 3*a* and 3*e*). Post hoc tests indicated that on day 7, oxygen consumption was significantly greater in cores with shells than in control cores. On day 21 when oxygen consumption was measured in all treatments, oxygen consumption was higher in cores with shells than in any other treatment, except the control. On day 14, sediment oxygen consumption did not differ among treatments, though there was a trend of higher consumption in the shell treatment, consistent with days 7 and 21 (Table 1, Fig. 3*c*). Oxygen consumption by mussels could only be compared on day 21 when destructive sampling occurred and did not differ among treatments (Table 1, Fig. 3*f*)

On days 7 and 14, mean oxygen consumption by sediments was 35 and 38 $mg \cdot m^{-2} \cdot h^{-1}$, respectively, while the mean consumption by mussels (zebra mussels in the water column only) was 45 and 36 $mg \cdot m^{-2} \cdot h^{-1}$, respectively. Thus, on these dates the presence of mussels approximately doubled the rate of benthic oxygen consumption. On day 21, the mean oxygen consumption by sediments was 82 $mg \cdot m^{-2} \cdot h^{-1}$, while the mean consumption by mussels was 32 $mg \cdot m^{-2} \cdot h^{-1}$, yielding a 42% increase in benthic oxygen demand due to mussel presence.

Nutrient fluxes

Water column concentrations of ammonium and SRP increased with time in all cores, indicating a net release of ammonium by sediments and mussels. Ammonium flux from sediments was higher in the shell treatment than for cores with zebra mussels in the water column, but neither treatment differed significantly from controls (Table 1, Fig. 4*a*). However, ammonium flux from mussels did not differ among treatments (Table 1, Fig. 4*b*). SRP flux from sediments did not differ among treatments (Table 1, Fig. 4*c*). However, zebra mussels located in the water column released significantly less SRP than either zebra or quagga mussels located on the sediment (Table 1, Fig. 4*d*). Nitrate+nitrite fluxes did not differ significantly by treatment for either sediments or mussels (Table 1, Figs. 4*e*–4*f*). Data on mussel nutrient release from one Z-sediment core and one Q-sediment core were excluded from the results because of errors in sample collection.

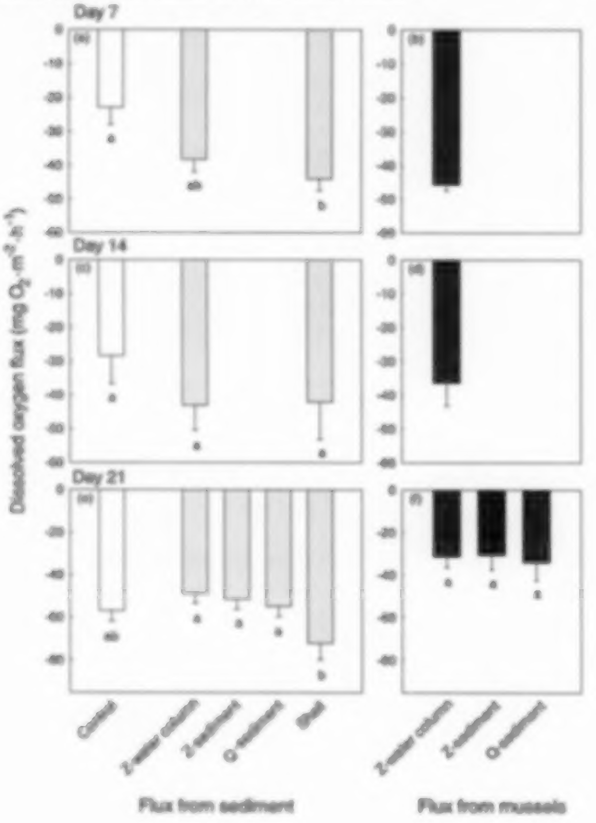
Ammonium and SRP flux from mussels were significantly different from zero for all treatments (*t* test, $p < 0.01$ in all cases). However, while average values for nitrate+nitrite release from mussels were generally positive, none differed significantly from zero (*t* test, $p > 0.4$ for all treatments). Ammonium release from mussels was 2.3 mg NH_4^+-$N \cdot m^{-2} \cdot h^{-1}$, while flux from sediments was 2.0 mg NH_4^+-$N \cdot m^{-2} \cdot h^{-1}$, indicating that mussel presence approximately doubled total benthic ammonium flux. Mean SRP flux from sediments was 1.0 mg PO_4^{3-}-$P \cdot m^{-2} \cdot h^{-1}$. Zebra mussels in the water column produced an average of 0.42 mg PO_4^{3-}-$P \cdot m^{-2} \cdot h^{-1}$, while zebra and quagga mussels on the sediments produced 1.3 and 1.4 mg PO_4^{3-}-$P \cdot m^{-2} \cdot h^{-1}$, respectively. Thus, mussels increased benthic SRP release by 42%–140%.

The N:P ratio of mussel release was higher for cores with zebra mussels suspended in the water column (molar N:P ≈ 11:1) than for either zebra mussels or quagga mussels on the sediment surface (molar N:P ≈ 4:1, df = 5, $F = 12.6$, $p = 0.0071$, Fig. 5). N:P ratios did not differ between zebra and quagga mussels (Tukey's test, Fig. 5). Nitrate+nitrite excretion from mussels were not included in N:P calculations because nitrate+nitrite flux did not differ significantly from zero.

Estimated nutrient release due to respiration

In all treatments, nitrogen flux predicted based on respiration differed from the observed excretion of nitrogen by 20% or less (Table 2). Zebra mussels in the water column released 50% more SRP than predicted, but zebra and

Fig. 3. Dissolved oxygen flux (mean + standard error) in microcosm experiments. Letters within each panel indicate significant differences (Tukey's test, $p < 0.05$) among treatments. Panels (*a*), (*c*), and (*e*) show the consumption rate by sediments for control (open bars) and mussel (gray bars) treatments. Panels (*b*), (*d*), and (*f*) show oxygen consumption by the mussels (solid bars). Values for Z-sediment (i.e., zebra mussels) and Q-sediment (i.e., quagga mussels) were not measured on days 7 and 14 to avoid any possible disruption to the sediments by removing mussels.



quagga mussels located on the sediment surface released 300% more SRP than predicted based on oxygen consumption (Table 2).

Discussion

Mussels located directly on the sediments, whether zebra or quagga, released significantly more SRP and did so at a lower N:P ratio than zebra mussels in the water column. Since the rates of nutrient release from the mussels were calculated by subtracting benthic fluxes in the presence or absence of mussels, the elevated SRP release observed in mussels on the sediments could conceivably be due either to a transient alteration to flux from the sediments or to a change in the excretion by the mussels. The possibility of a transient alteration to sediment flux seems unlikely. Since sediments from which mussels were removed did not differ from control sediments, any alteration to sediment flux

Fig. 4. Rates of nutrient flux (mean + standard error) in experimental cores at completion of experiment. Letters within each panel indicate significant differences (Tukey's test, $p < 0.05$) among treatments. Panels (*a*), (*c*), and (*e*) show the nutrient flux rate for sediments in control (open bars) and mussel (gray bars) treatments. Panels (*b*), (*d*), and (*f*) show nutrient release by the mussels (solid bars).

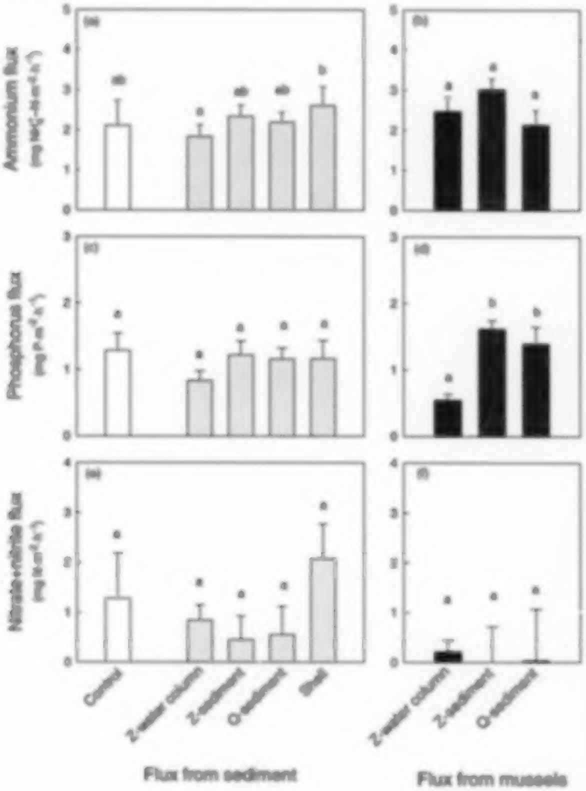


Fig. 5. N:P molar ratio (mean + standard error) of mussel excretion. Letters indicate significant differences (Tukey's test, $p < 0.05$) among treatments.

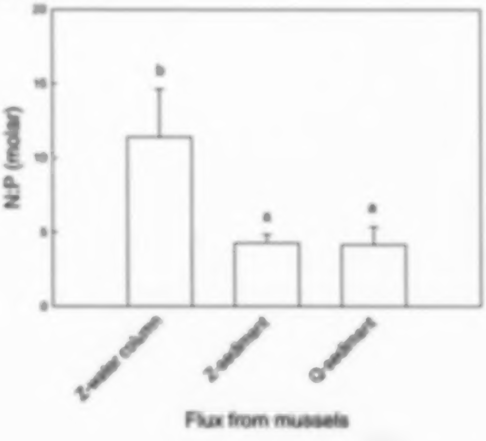


Table 2. Comparison of measured rates of ammonium and soluble reactive phosphorus (SRP) release by mussels to release rates predicted based on oxygen consumption by mussels (Z, zebra mussels; Q, quagga mussels).

	Ammonium release by mussels ($\mathrm{mg\ N\cdot m^{-2}\cdot h^{-1}}$)		SRP release by mussels ($\mathrm{mg\ P\cdot m^{-2}\cdot h^{-1}}$)	
	Predicted	Measured	Predicted	Measured
Z-water column	2.07	2.18	0.29	0.42
Q-sediment	2.02	2.13	0.28	1.39
Z-sediment	2.25	2.70	0.31	1.31

would have had to disappear immediately upon removal of the mussels. More likely, the differences in SRP release are due to alterations in mussel excretion. Hecky et al. (2004) hypothesized that zebra mussels release iron-bound phosphorus from the particles they ingest because of the anoxic conditions in their guts. It is likely that mussels filter feeding directly at the sediment surface ingest more sediment particles, potentially releasing the iron-bound phosphorus in these particles. The reduction of iron-bound phosphorus to a soluble dissolved state could increase primary productivity by transforming phosphorus into a form that is available to phytoplankton in the water column (Carpenter et al. 1992).

The hypothesis that SRP is being released because of ingestion of sediment particles is supported by calculations indicating that the additional SRP cannot be accounted for by food intake (Table 2). Although using oxygen consumption to predict nutrient excretion requires several assumptions, this approach predicted ammonium release values very similar to the measured values, indicating that the assumptions are likely to be reasonable. However, the phosphorus released through respiration of organic matter can only account for one-fourth of the SRP released by mussels on the sediment. This implies that the elevated amounts of SRP released by mussels on the sediments must come from a source other than food. Since SRP release by zebra mussels that were not in direct contact with sediments matched predicted SRP release much more closely, the source of additional SRP is likely to be associated with the sediments.

The mobilization of phosphorus from lake sediments by dreissenid mussels has important implications for the cycling of phosphorus in lakes. Such a mobilization would contribute to the increased availability of SRP observed in many invaded systems (i.e., Effler et al. 1996; Makarewicz et al. 2000). This mechanism implies that systems with high levels of iron-bound phosphorus in the sediments would be particularly likely to exhibit increases in SRP concentration in response to invasion. The SRP levels could also continue to increase over time as additional SRP is released from the sediments. This is consistent with the pattern of continuous gradual increase in water column SRP observed in Oneida Lake, though many other factors, such as changes in phosphorus input from the watershed or alterations in the dynamics of primary producers, could also cause this increase. Another important implication of SRP release from the sediments is that the subsequent invasion of quagga mussels, which occupy soft sediment habitats at greater density than zebra mussels (Mills et al. 1996), could generate further changes in nutrient dynamics, even in lakes previously invaded by zebra mussels. This is consistent with the pattern observed in Cayuga Lake, New York, where hypolimnetic SRP concentrations did not increase with the arrival of zebra mussels, but began to rise only after the subsequent invasion of quagga mussels (Upstate Freshwater Institute 2006). If this pattern holds, SRP levels in Oneida Lake could begin to increase more rapidly because of the invasion of quagga mussels, which were first observed in Oneida Lake in 2008. Given the potential implications for lake ecosystems, the hypothesis that iron-bound phosphorus from sediments is released in the anoxic guts of dreissenid mussels is an important area for future research. My results are consistent with this mechanism but do not confirm that anoxic guts are the actual location of the process.

Studies of zebra and quagga mussel excretion rates in which the mussels are not in direct contact with the sediments may underestimate the rate of SRP production. The N:P ratio of excretion for mussels not in direct contact with sediments (≈11:1) found in this experiment is similar to those observed by Arnott and Vanni (1996). However, when mussels were living directly on the sediment, the N:P ratio of their excretion (≈4:1) was substantially lower than the excretion N:P ratios observed by Arnott and Vanni (1996) for similarly sized mussels over a similar time span. Quagga mussels had similar per mussel excretion rates to zebra mussels, but higher per mass excretion rates (all mussels had a shell length of 10–15 cm, but the wet mass with shell of the zebra mussels was twice that of the quagga mussels). This pattern differs from a previous study, which found that zebra mussels excrete higher levels of SRP per soft tissue biomass than quagga mussels (Conroy et al. 2005*a*). However, it is consistent with the observation that zebra and quagga mussels have similar per mussel feeding rates (Baldwin et al. 2002).

In the current experiment, direct excretion by dreissenid mussels was the predominant effect of mussels on benthic nutrient flux. Indeed, the mussels had no measurable effect on sediment flux of ammonium, SRP, or nitrate+nitrite. This differs from observations in previous microcosm studies that sediments beneath zebra mussel colonies exhibited increased nitrification and denitrification rates (Bruesewitz et al. 2008) and changes in nitrate and phosphate flux from sediments (Bykova et al. 2006).

As with nutrients, the primary influence of the mussels on benthic oxygen demand was the direct consumption of oxygen by the mussels, rather than altered sediment uptake. Sediments underlying mussel colonies exhibited the same rate of oxygen consumption as control sediments. However, oxygen consumption was elevated in microcosms with empty mussel shells, indicating that accumulation of mussel shells in the sediments may increase benthic oxygen consumption. Several mechanisms could explain this increase. The shells provide additional surface area for deposition and biofilm development, which could increase oxygen consumption. Alternatively, decomposition of any residual organic matter on the shells could also consume oxygen. Regardless of mechanism, the increased oxygen consumption could be important to lake ecosystems, since substantial volumes of mussel shell material can accumulate on the sediment surface, particularly in systems with high levels of dissolved calcium (Strayer and Malcom 2007). While the change in oxygen demand due to shells is small relative to the direct consumption of oxygen by mussels, this effect could be important on a lake-wide basis because shells can accumulate across much of the benthic surface, including areas not inhabited by live mussels (Zaiko et al. 2009).

It is important to note that all results in this study were from short-term microcosm experiments. Different patterns might be observed over longer time scales because of continued gradual changes in sediments. Several ecological interactions that were not incorporated in the microcosms could also influence benthic nutrient flux. Different mussel densities could have differing effects on nutrient dynamics. In addition, invasion of dreissenid mussels alters communities of both benthic invertebrates (Ward and Ricciardi 2007) and benthic primary producers (Zhu et al. 2006). Both communities can influence nutrient dynamics (Carpenter et al. 1992; Mermillod-Blondin and Rosenberg 2006), which could modify the net impact of dreissenid mussels on benthic nutrient cycling.

Direct excretion by mussels, rather than alteration of sediment fluxes, is likely the main mechanism for alteration of benthic oxygen and nutrient fluxes by dreissenid mussels, at least over the temporal and spatial scales of the microcosm experiments presented here. One exception to this may be increased oxygen demand in sediments containing accumulated empty mussel shells. The increase in the rate of phosphorus release is particularly dramatic when mussels colonize soft sediments directly. Interaction of dreissenid mussels with lake sediments appears to allow mobilization of sediment phosphorus, potentially contributing to a variety of ecosystem changes that have been observed in invaded lakes. Dreissenid invasion has been associated with lake-wide increases in SRP availability (Makarewicz et al. 2000; Conroy et al. 2005*b*) and increases in harmful cynaobacterial blooms (Vanderploeg et al. 2001; Raikow et al. 2004) and *Cladophora* abundance (Higgins et al. 2008).

By dramatically increasing the benthic fluxes of ammonium and SRP, dreissenid mussels are potentially altering the nutrient dynamics of lake ecosystems. This is particularly important in shallow, polymictic lake systems such as Oneida Lake (Mills et al. 1978), where the ratio of benthic area to volume is high and benthic fluxes of nutrients are rapidly made available to phytoplankton. If, as is indicated by this study, mussels are mobilizing sediment phosphorus, SRP levels may continue to increase in invaded ecosystems, even if mussel biomass remains the same. This in turn could lead to even greater prevalence of *Microcystis*, *Cladophora*, and other nuisance species.

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Direct versus indirect pathways of salmon-derived nutrient incorporation in experimental lotic food webs

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Abstract: The objective of our study was to examine how salmon carcass subsidization through alternative trophic pathways affected stream food web productivity. Three salmon carcass treatments (dissolved carcass nutrients only, dissolved carcass nutrients + carcass material, and a carcass-free control) were replicated five times in artificial stream channels. We quantified changes in water chemistry and the production of periphyton, macroinvertebrates, and age 0+ steelhead trout (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) over 65 days. Dissolved ammonium and periphyton chlorophyll *a* concentrations increased for an approximate 2-week period in both carcass-augmented treatments. However, there was no commensurate effect on periphyton ash-free dry mass. Total macroinvertebrate biomass was significantly greater in the presence of nutrients + material after 65 days, but no such increase was observed in response to the addition of dissolved nutrients only. Despite modest and inconsistent effects at lower trophic levels, both the nutrients only and nutrients + material treatments increased the growth and condition of age 0+ steelhead trout, with significantly greater gains occurring in the presence of nutrients + material. These data suggest that while salmon carcasses can enhance the short-term growth of juvenile salmonids via bottom-up pathways, the availability and direct consumption of carcass biomass may promote a substantial amount of additional production.

Résumé : L'objectif de notre étude est d'examiner comment les apports des carcasses de saumons à travers des voies trophiques de rechange affectent la productivité des réseaux alimentaires dans les cours d'eau. Trois traitements expérimentaux avec des carcasses de saumons (nutriments dissous des carcasses seuls, nutriments dissous des carcasses + matériaux des carcasses, témoins sans carcasse) ont été répétés cinq fois dans des canalisations artificielles d'eau courante. Nous avons mesuré les changements de chimie des eaux, ainsi que la production du périphyton, des macroinvertébrés et des truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) d'âge 0+ pendant 65 jours. Dans les deux traitements contenant des carcasses, les concentrations d'ammonium dissous et de chlorophylle *a* du périphyton ont augmenté pendant une période d'environ 2 semaines. Il n'y a pas eu, cependant, d'effet du même ordre sur la masse sèche sans les cendres du périphyton. La biomasse totale de macroinvertébrés était significativement plus élevée en présence des nutriments + matériaux après 65 jours; cependant, l'addition des seuls nutriments dissous ne produit pas d'accroissement comparable. Malgré les effets modestes et irréguliers aux niveaux trophiques inférieurs, les traitements impliquant soit les nutriments seuls ou les nutriments + matériaux augmentent la croissance et la condition des truites arc-en-ciel anadromes d'âge 0+, avec des gains significativement plus élevés en présence des nutriments + matériaux. Nos résultats indiquent que, bien que les carcasses de saumons puissent accroître la croissance à court terme des jeunes salmonidés par des voies ascendantes, la disponibilité et la consommation directe de la biomasse des carcasses peuvent promouvoir une quantité important de production additionnelle.

[Traduit par la Rédaction]

Introduction

Our understanding of the ecological importance of salmon carcasses to freshwater ecosystems has vastly improved as a result of research conducted over the previous two decades. Empirical studies have established that salmon-derived nutrients and biomass (collectively termed SDN) enter stream food webs through two predominant pathways: (*i*) the base of the food chain via uptake of mineralized inorganic nutrients and (*ii*) at higher trophic levels through the direct consumption of salmon-derived material (primarily salmon eggs and carcass tissues) by aquatic consumers. However, uncertainty remains over the relative contribution of each pathway to the dynamics and productivity of organisms at different trophic levels (Gende et al. 2002; Brock et al. 2007; Monaghan and Milner 2008). Several studies have documented elevated dissolved stream nutrient concentrations associated with the presence of spawning salmon and

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the decomposition of salmon carcasses (e.g., O'Keefe and Edwards 2003; Mitchell and Lamberti 2005). Since many salmon-bearing streams are nutrient limited, dissolved SDN inputs may stimulate production of primary producers and heterotrophic microbes that serve as the energetic base of the food web and enhance overall trophic productivity from the bottom-up (Schuldt and Hershey 1995; Wipfli et al. 2003). Common proxies of primary production such as periphyton biomass or chlorophyll *a* content have been shown to increase in response to the addition of salmon carcasses in some studies (e.g., Wipfli et al. 1999; Mitchell and Lamberti 2005) but not others (e.g., Rand et al. 1992; Ambrose et al. 2004). In cases where enhanced primary production has been reported, such increases may translate into higher biomass or growth rates of aquatic macroinvertebrates (Minakawa 1997; Wipfli et al. 1998; Chaloner and Wipfli 2002) and resident fishes (Bilby et al. 1998; Wipfli et al. 2003). Furthermore, natural abundance stable isotope studies have highlighted the importance of bottom-up nutrient cycling in many recipient ecosystems and provided unambiguous evidence of salmon-derived carbon and nitrogen assimilation at multiple trophic levels (e.g., Kline et al. 1990; Bilby et al. 1996; Chaloner et al. 2002).

There is also evidence that direct consumption of carcass tissues and eggs by stream consumers represents an important pathway linking SDN to higher trophic levels (Bilby et al. 1996; Wipfli et al. 1999; Chaloner and Wipfli 2002). Salmon tissues and eggs are rich in minerals, biochemicals, and micronutrients (Mathisen et al. 1988) and may represent a nutritionally superior food resource for aquatic consumers (Heintz et al. 2004). Many aquatic macroinvertebrate taxa (Wipfli et al. 1998; Minakawa and Gara 1999; Monaghan and Milner 2008), stream-dwelling amphibians (Parker 1994), and fishes (Kline et al. 1993; Foote and Brown 1998) scavenge and ingest salmon carcasses or eggs when available. Bilby et al. (1998) reported that carcass-derived material accounted for 78% and 60% of the stomach contents of age 0+ steelhead trout (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*), respectively, during the period when carcasses were abundant. Moreover, they reported that fish reared in the presence of carcasses experienced increased growth relative to conspecifics in a nearby stream with few spawning salmon. Similarly, Wipfli et al. (2003) observed that carcass additions improved growth of age 0+ coho salmon in artificial channels and increased growth of Dolly Varden (*Salvelinus malma*) and cutthroat trout (*Oncorhynchus clarkii*) in a natural stream. High growth rates are important for juvenile salmonids because body size is a key determinant of overwinter survival (Hartman and Scrivener 1990; Quinn and Peterson 1996) and positively correlated with smolt to adult survival (Ward and Slaney 1988; Holtby et al. 1990).

Empirical studies conducted across the northern Pacific Rim have provided evidence that nutrients and biomass delivered by anadromous salmon can have profound effects on the ecology of freshwater and riparian ecosystems. However, diminished or extirpated salmon populations have greatly reduced the current influx of SDN to many watersheds (Gresh et al. 2000), and resource managers have become increasingly concerned that this nutrient deficit may be limiting the production of juvenile salmon (Wipfli et al. 2004). This has prompted many local, state, and federal agencies to employ nutrient mitigation measures such as the addition of inorganic fertilizers (Ashley and Stockner 2003; Wilson et al. 2003), surplus hatchery carcasses (Lackey 2003; Missildine 2005), or carcass analogues (Kohler et al. 2008). However, the short- and long-term efficacy of nutrient augmentation programs is poorly understood (Claeson et al. 2006), and robust evidence for a positive relationship between SDN and the production of juvenile salmonids remains limited (Schindler et al. 2003; Wilzbach et al. 2005).

The objective of this study was to determine how SDN subsidization through direct and indirect trophic pathways affected stream food web structure and productivity. To that end, we added two forms of salmon carcass-derived resources to experimental stream channels (i.e., whole carcasses and carcass leachate only) and examined changes in water chemistry and the production of periphyton, macroinvertebrates, and juvenile salmon over 65 days. Our hypotheses were that (*i*) the addition of salmon carcass-derived leachate results in increased productivity at all trophic levels, and (*ii*) increases in productivity are greatest when both dissolved nutrients and carcass-derived material (i.e., salmon flesh and eggs) are available as trophic resources. Our aim is to improve understanding of how salmon carcass-derived biomass affects the short-term dynamics of lotic communities and the growth of juvenile salmonids.

Materials and methods

Study site

This study was conducted in the North Branch of the North Fork Navarro River (drainage area 161 km^2), a fourth-order stream in Mendocino County, California, USA (39°10′N, 123°33′W). The climate is Mediterranean with an average annual precipitation of 124 cm, most of which falls between October and May. Following spring rains, streamflow gradually decreases to a late summer base flow of <0.04 m^3·s^{-1} at our study site. The surrounding catchment is a 40- to 80-year-old mixed conifer forest dominated by coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*). Common riparian species include red alder (*Alnus rubra*), tanoak (*Lithocarpus densiflorus*), California laurel (*Umbellularia californica*), and bigleaf maple (*Acer macrophyllum*). The fish assemblage is entirely native and includes steelhead trout, coho salmon, Pacific lamprey (*Lampetra tridentata*), Navarro roach (*Lavinia symmetricus navarroensis*), coastrange sculpin (*Cottus aleuticus*), prickly sculpin (*Cottus asper*), and threespine stickleback (*Gasterosteus aculeatus*).

Like many Pacific Northwest watersheds, the Navarro River has experienced a marked reduction in anadromous salmonid and lamprey populations. Although quantitative population data are unavailable, historical records indicate that coho salmon once occupied >210 km of the Navarro River and its tributaries (Brown and Moyle 1991). Presently, however, coho only inhabit ~20% of their historic distribution in these same basins (Johnson et al. 2002). The Navarro River is also representative of many small coastal California watersheds in that a sand bar forms across the mouth of the river each summer (see Shapovalov and Taft 1954). This barrier precludes returning adult salmon from entering fresh water until heavy rains generate sufficient streamflow to breach the sand bar. Among the ecological consequences of this annual barrier are that the timing of freshwater entry by both anadromous coho salmon and steelhead is highly variable, and spawning fish are often present for protracted periods (i.e., January–May) relative to salmon-bearing watersheds at more northern latitudes.

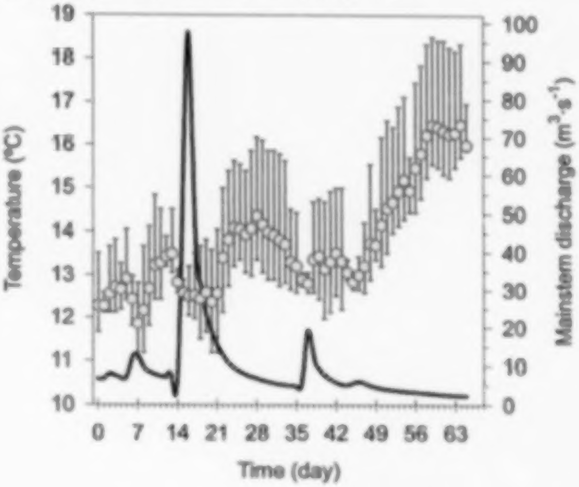
Experimental design

In the spring of 2005, in situ flow-through artificial stream channels were used to assess how SDN subsidization through alternative trophic pathways affected aquatic food web structure and stream productivity. Fifteen experimental channels (244 cm long × 30.5 cm wide × 40.6 cm high) were fabricated from 9 mm clear acrylic and consisted of a solid bottom pane and two solid side panels. Channels were arranged side-by-side in five groups of three with a 30 cm access aisle between the groups and their long axes parallel to streamflow. Channels were supported by a 6.1 m × 2.1 m wooden frame that was buried flush with the riverbed and anchored with rebar. Each channel received a 10 cm layer of substrate (primarily gravel and cobble) excavated from the riverbed, and water was provided via natural streamflow. Water velocity in each channel was measured every 7 days using a Flo-Mate model 2000 velocity meter (Marsh-McBirney, Frederick, Maryland, USA) and averaged 0.46 $m \cdot s^{-1}$ (range = 0.38 to 1.68 $m \cdot s^{-1}$). Although water velocity was temporally variable it was not substantially different among channels or treatments on any date. Water temperature was continuously measured (30 min intervals) using Optic StowAway temperature dataloggers (maximum error: ±0.25 °C; Onset Computer Corp., Bourne, Massachusetts, USA) positioned near the outflow of each channel. Water temperature averaged 13.7 °C with a range of 11.0–18.4 °C (Fig. 1). Riparian canopy closure above each channel was estimated prior to the start of the experiment using a convex spherical densitometer. Canopy closure averaged 29% (standard deviation, SD = 11) and was not significantly different among channels or treatment groups. Channels were positioned in the stream on 5 April, 28 days prior to the start of the experiment, to allow for natural accumulation of organic matter and colonization by stream macroinvertebrates.

On 3 May channel ends were screened with Vexar plastic netting (4.0 mm aperture) and subsequently stocked with five age 0+ steelhead trout captured via electrofishing from a nearby tributary. Prior to being placed in the stream channels (hereafter enclosures), individual fish were anaesthetized with clove oil, weighed (wet mass ± 0.01 g), measured for fork length (FL ± 0.5 mm), and distinctively marked using multiple visible implant elastomer (VIE) tags (Northwest Marine Technology, Shaw Island, Washington, USA). Steelhead trout (range = 36–52 mm FL; 0.37–1.21 g) were deliberately size-matched among enclosures to ensure analogous initial biomass.

The 15 enclosures were subsequently assigned to one of three experimental treatment groups: (*i*) salmon-derived material + nutrients, (*ii*) salmon-derived nutrients only, and (*iii*) no salmon-derived material or nutrients (control treatment) yielding five replicates per treatment. Specifically, enclosures treated with salmon-derived material + nutrients (hereafter CARCASS treatment) received a freshly spawned-out (i.e., free of fungal growth and visible signs of decay) adult coho salmon carcass. Carcasses were collected from various Navarro River tributaries between 23 January and 9 March 2005. Harvested carcasses were measured (wet mass and FL) and sexed in the field before being placed on dry ice and transported to the laboratory for storage at –80 °C. In the laboratory, carcasses were cut into three sections (head, body, and tail) by making transverse cuts (*i*) midway between the posterior-most point on the operculum and the first ray of the dorsal fin and (*ii*) midway between the last dorsal fin ray and the adipose fin. Mean (±1 standard error, SE) masses of the resultant sections were 1.07 ± 0.36, 1.29 ± 0.11, and 0.52 ± 0.05 kg for head, body, and tail segments, respectively (*n* = 10 each). Only female carcasses were used in our experiment, and initial biomass loadings were standardized to 2.24 ± 0.01 kg wet mass by adding one head, body, and tail section to each treated enclosure. This loading rate approximates the mean mass of adult coho carcasses in the Navarro River watershed (J.D. Kiernan, unpublished data) and was selected to ensure a salient nutrient pulse through each experimental unit. Carcass sections were tethered to the substrate at the upstream end of each enclosure and allowed to naturally decompose over the course of the experiment. The natural breakdown process resulted in a supply of dissolved inorganic nutrients, dissolved organic matter, and particulate matter (fragments of salmon flesh and few residual eggs) to food web constituents. All carcass introductions were assumed to be equal in terms of nutrient content.

Fig. 1. Time series of mean daily stream water temperature (circles) and mainstem Navarro River discharge (solid line) during the 65-day experimental period (3 May to 7 July 2005). Water temperature was recorded directly from each experimental stream channel. Vertical bars indicate daily minima and maxima. Discharge data were derived from USGS gaging station 11468000 located ~18 km downstream of our study site.



Enclosures treated with only dissolved salmon-derived nutrients (hereafter NUTRIENT treatment) received analogous salmon carcass sections that were first sewn into 45 cm × 30 cm Nitex mesh bags (5.0 µm pore size) and tethered to the channel substrate near the inflow. Nitex bags permitted dissolved carcass nutrients to leach into the channel while preventing direct colonization and ingestion of carcass-derived material by invertebrates and fish. By eliminating the direct consumption of carcass material, any observed differences in trophic productivity (relative to experimental controls) were assumed to represent bottom-up processes exclusively. Enclosures assigned to the CONTROL treatment received no carcass additions. Treatments were introduced on 3 May (day 0) and the experiment was terminated after 65 days.

On 18 May (day 15), a high streamflow event caused the river to breach the top of the enclosures (Fig. 1) and resulted in the death or loss of 6, 8, and 9 fish from the CONTROL, NUTRIENT, and CARCASS treatments, respectively. Following river recession on 21 May, missing individuals were replaced with fish of the appropriate size as determined from the size distribution of surviving individuals in CONTROL treatment enclosures. Replacement fish were not marked with VIE tags prior to introduction, and we assumed that this decision would not affect either their behavior or performance relative to tagged individuals. Fish introduced after day 0 were excluded from all growth-related analyses.

Field sampling

Water chemistry

Stream water was collected from the downstream end of each enclosure immediately prior to carcass introductions (day 0), at 2-day intervals for the first 14 days, and at 7-day intervals thereafter (*n* = 14 dates). Samples were collected into polypropylene bottles and stored at –30 °C until analysis. Following the final collection date, samples were thawed and analyzed for dissolved ammonia (NH_4^+), nitrite+nitrate (hereafter nitrate or NO_3^-), and soluble reactive phosphorus (SRP) using a Lachat QuikChem 8000 Flow Injection Analyzer (Hach Company, Loveland, Colorado, USA). SRP was determined using the molybdate–antimony reaction followed by ascorbic acid reduction (method detection limit (MDL) = 0.3 μg P·L^{-1}). NO_3^- was determined using the cadmium reduction–diazotization method (MDL = 0.25 μg N·L^{-1}), and ammonium was determined using the phenolate method (MDL = 2.0 μg N·L^{-1}). Total nitrogen (TN) was quantified after conversion to nitrite with an alkaline persulfate digestion and subsequent flow injection analysis as outlined above (MDL = 0.5 μg N·L^{-1}). Total organic carbon (TOC) concentrations were determined by high-temperature combustion (MDL = 1 mg·L^{-1}) using a Shimadzu 5000A total carbon analyzer (Shimadzu Corp., Kyoto, Japan). Total inorganic nitrogen (TIN) was calculated as the sum of NH_4^+-N and NO_3^--N. Total organic nitrogen (TON) was calculated by subtraction of TIN from TN.

Periphyton sampling

Unglazed ceramic tiles (40.3 cm^2) were used as standardized substrates for periphyton sampling. Periphyton accrual began on 19 March when 300 tiles were placed in a side channel of the main river containing slack water. On 5 April, 20 tiles were randomly selected for transfer to each experimental enclosure where they continued to incubate in situ for an additional 28 days. Periphyton was sampled immediately prior to carcass introductions and at weekly intervals until the end of the experiment (*n* = 10 dates). On each sample date, two randomly selected tiles were removed from each enclosure to quantify ash-free dry mass (AFDM) and chlorophyll *a* (Chl *a*) content. In the laboratory, tile surfaces were examined under 10× magnification, and all invertebrates encountered were removed and discarded. The upper surface of each tile was then scraped with a razor blade, and dislodged material was collected on precombusted (500 °C for 4 h) glass-fiber filters (GF/F; 47 mm diameter, 0.7 μm effective pore size). Filters were analyzed for chlorophyll content using a Turner Quantech FM109525 fluorometer (Barnstead-Thermolyne Corp., Dubuque, Iowa, USA) after extraction in 20 mL of 90% methanol for 24 h at 4 °C. Fluorometric excitation and emission wavelengths were 450 nm and 670 nm, respectively. Following pigment extraction, filters were transferred to aluminum weigh dishes, oven-dried to a constant mass (≥48 h at 60 °C), ashed for 4 h at 500 °C, and reweighed to determine AFDM (Steinman et al. 2006). To evaluate the relative contribution of autotrophic versus heterotrophic biomass to the periphyton community, we calculated the autotrophic index (AI) for each sample using the following formula:

$$(1) \qquad \mathrm{AI} = \frac{\mathrm{AFDM}\ (\mathrm{mg \cdot cm^{-2}})}{\mathrm{Chl}\ a\ (\mathrm{mg \cdot cm^{-2}})}$$

Macroinvertebrate sampling

Benthic macroinvertebrates were quantitatively sampled from each enclosure using a modified 20 cm diameter Hess sampler (363 μm mesh) to a depth of 10 cm. Samples were collected immediately prior to carcass introductions and at 35 and 65 days after introduction. Net contents were passed through a 500 μm sieve, and retained material was placed on ice and transported to the laboratory for identification and enumeration. In the laboratory, macroinvertebrates were identified to the lowest practical taxonomic unit (genus or species in most cases) using Merritt and Cummins (1996); Smith (2001), and Thorp and Covich (2001). Larval Chironomidae were slide-mounted in Euparal medium and identified to genus when possible using Wiederholm (1983) and Merritt and Cummins (1996). Each taxon was assigned to a general trophic or functional feeding group (FFG) according to Merritt and Cummins (1996). FFGs included collector–gatherers, collector–filterers, scrapers, shredders, predators, and omnivores. To obtain macroinvertebrate biomass estimates, unpreserved samples were oven dried to a constant mass (55 °C for ≥ 48 h) and weighed (±1.0 μg) using a PerkinElmer AD-4 auto-balance (PerkinElmer, Waltham, Massachusetts, USA). Chironomid standing crop was estimated by measuring the lengths of slide-mounted individuals to the nearest 0.001 mm with a compound video microscope and Optimus image analysis system (Media Cybernetics, Inc. Silver Spring, Maryland, USA). Chironomid lengths were converted to biomass estimates using published length–mass relationships (Smock 1980; Nolte 1990). We summarized benthic macroinvertebrate data in terms of density (organisms·0.1 m^{-2}), taxon richness, diversity (Simpson's reciprocal index, 1/*D*), FFG proportions, and total biomass (mg dry mass (DM)·0.1 m^{-2}). Simpson's reciprocal diversity index was calculated as

$$D = \frac{1}{\sum p_i^2} \tag{2}$$

where D is diversity and p_i the proportion of individuals in the ith taxon in the total sample.

To assess the flux of emerging aquatic invertebrates, we fit each enclosure with a single square-pyramid emergence trap that sampled an area of 0.093 m^2. Emergence was quantified at days 14, 35, 56, and 65 after deploying traps for the 7 consecutive days preceding each collection. Captured invertebrates were frozen on dry ice and returned to the laboratory for enumeration and biomass determination. We made no attempt to determine the taxonomic composition of emergence samples. Data were expressed as mean emergence rate (individuals·(0.1 m^{-2})·day^{-1}) and mean emergent dry mass (mg DM·(0.1 m^{-2})·day^{-1}) for each treatment on each sample date.

Fish sampling

Upon termination of the experiment, all age 0+ steelhead trout were removed from enclosures, positively identified, weighed, measured, and frozen using liquid nitrogen. Condition factor (K) was calculated for each fish using the equation

$$K = \frac{M \times 10^5}{L^3} \tag{3}$$

where M is mass (g) and L is fork length (mm). We also calculated standardized mass specific growth rates (MSGR; Ω) which account for the effects of fish size on growth rate using the equation presented by Ostrovsky (1995):

$$\Omega = \frac{M_2^b - M_1^b}{b \times \text{days}} \times 100 \tag{4}$$

where M_1 and M_2 are mass at the start and end of the growth period, respectively, and b is the allometric mass exponent for the relation between specific growth rate and body mass. This exponent has been estimated to be 0.34 for steelhead trout acclimated to 15 °C (Wangila and Dick 1988). MSGR reports growth as a percent change in mass per gram of body mass per day (%·g^{-1}·day^{-1}).

Data analysis

Data were transformed as appropriate to correct for heteroscedasticity and non-normality. Differences in macroinvertebrate total density, richness, diversity, and FFG proportions among treatments were assessed using analysis of covariance (ANCOVA) with pretreatment values (samples collected on day 0) as the covariate. Treatment differences in macroinvertebrate total biomass and the densities of individual taxa were assessed at days 35 and 65 using analysis of variance (ANOVA). To test for treatment effects on age 0+ steelhead MSGR and K, ANOVAs were performed using type IV sum of squares from the general linear models procedure in SAS (version 9.1.3; SAS Institute Inc., Cary, North Carolina, USA) to account for empty cells and nonorthogonal data. We set our experiment-wise type I error rate (α) at 0.05 and used Bonferroni–Holm (step-down) adjusted p values when tests involved multiple comparisons. Tukey's honestly significant difference (HSD) test was used to test for differences between treatments when a significant overall treatment effect was found.

Treatment differences in periphyton response variables (Chl *a* content, AFDM, and AI values), invertebrate emergence (rate and biomass), and stream water SRP, TN, N:P, and TOC were examined using repeated measures (rm) ANOVA with treatment and time as fixed effects. We report Greenhouse–Geisser adjusted p values for time and time × treatment interactions to account for potential violations of sphericity. Measurements of stream water NH_4^+ and NO_3^- contained many values at or below method detection limits (i.e., data were left censored) and could not be normalized to meet the assumptions of rmANOVA. Therefore, we pooled measurement of NH_4^+ and NO_3^- across all sample dates and used the nonparametric method outlined by Helsel (2005) to test for treatment effects. Specifically, left-censored data distributions were rescaled (flipped) to right-censored distributions so that empirical cumulative distribution functions could be generated and compared using log-rank tests developed for survival analysis by Kaplan and Meier (1958). We used the Peto–Peto weight function, which is sensitive to higher values in left-censored data (equivalent to early failures in right-censored survival analysis) and advocated for lognormally distributed environmental data sets (Lee 1992). A significant overall test was followed by pairwise comparisons of treatments using the same methods. Rescaling, generation of distribution functions, and hypothesis testing of NH_4^+ and NO_3^- were performed using NADA and survival add-on packages (Lee 2007) for the R statistical computing environment (R Development Core Team 2008). All other statistical tests were conducted using SAS or NCSS software version 2004 (NCSS, Kaysville, Utah, USA).

Results

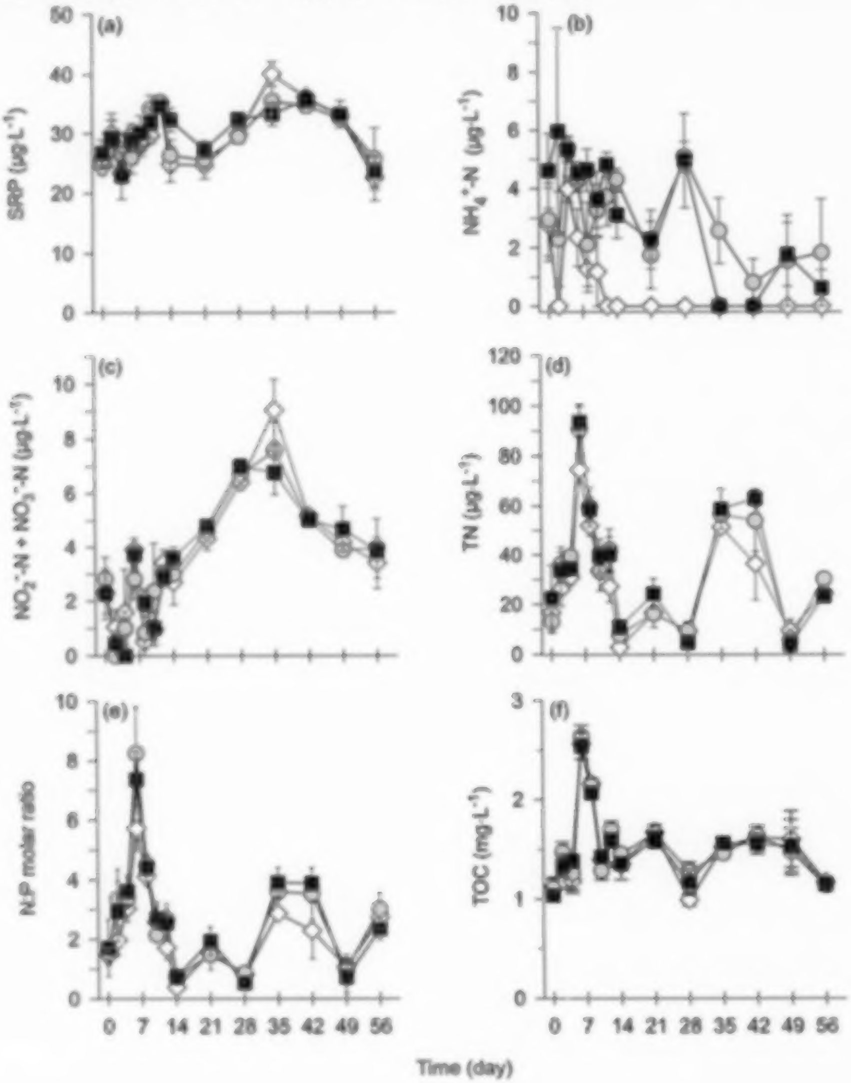
Water chemistry

Of the water chemistry variables measured, only NH_4^+ concentration exhibited a significant response to treatments (log-rank test, $\chi^2 = 34.4$, df = 2, $p < 0.01$). The distribution of NH_4^+ measurements in CARCASS and NUTRIENT treatments were different from the CONTROL treatment over the course of the study (log-rank tests, $\chi^2 = 32.8$ and 28.4, respectively, df = 1, $p < 0.01$ for both), but not different from each other ($p = 0.82$; Fig. 2*b*). All other analytes varied considerably between sample dates, but concentrations were not significantly different among treatments (log-rank test for NO_3^-, $p = 0.92$; rmANOVA treatment effects for SRP, TN, N:P, and TOC: all $p > 0.05$; Fig. 2).

Periphyton

There was an overall treatment effect on mean periphyton Chl *a* content (rmANOVA $F_{[2,12]} = 7.38$, $p < 0.01$), but no consistent temporal trend associated with this difference (rmANOVA treatment × time, $F_{[18,108]} = 1.06$, $p = 0.40$; Fig. 3*a*). We found no evidence that carcass augmentation affected either periphyton AFDM (rmANOVA treatment effect, $F_{[2,12]} = 0.05$, $p = 0.96$; Fig. 3*b*) or AI values (rmANOVA treatment effect, $F_{[2,12]} = 2.68$, $p = 0.11$; Fig. 3*c*) over the course of the experiment.

Fig. 2. Time series of stream water nutrient concentrations for (*a*) soluble reactive phosphorus, (*b*) ammonium, (*c*) nitrite+nitrate, (*d*) total nitrogen, (*e*) molar ratio of nitrogen to phosphorus, and (*f*) total organic carbon. Symbols represent mean values ±1 standard error for carcass (black squares), nutrient (gray circles), and control (open diamonds) treatment groups.



Benthic macroinvertebrates

While carcass subsidies had no effect on total macroinvertebrate biomass on day 35 (ANOVA, $F_{[2,12]} = 1.39$, $p = 0.29$), mean biomass was greater in the CARCASS treatment than in the CONTROL at experiment's end (ANOVA, $F_{[2,12]} = 6.16$, $p = 0.01$; Tukey's HSD, $p < 0.05$; Fig. 4*b*). A similar temporal pattern was observed for macroinvertebrate diversity, with no effect on day 35, and significantly higher diversity in the CONTROL than CARCASS treatment on day 65 (ANCOVA, $F_{[2,11]} = 7.49$, $p < 0.01$; Tukey's HSD, $p < 0.05$; Fig. 4*d*). We found no difference in total macroinvertebrate density or taxonomic richness among treatments at any time during the experiment (Figs. 4*a*, 4*c*). Macroinvertebrate assemblages in all treatments were numerically dominated by members of the collector–gatherer feeding guild, which comprised over 55% of the assemblages on both sampling dates (Fig. 5*b*). However, the proportion of collector–gatherers was significantly greater in the CARCASS and NUTRIENT treatments than in the CONTROL on both day 35 (ANCOVA, $F_{[2,11]} = 5.14$, $p = 0.03$; Tukey's HSD, $p < 0.05$) and day 65 ($F_{[2,11]} = 5.92$, $p = 0.02$; Tukey's HSD, $p < 0.05$; Fig. 5*b*). Two macroinvertebrate FFGs exhibited significant differences in proportional abundance on day 35 and not day 65: scrapers were less abundant in the CARCASS treatment (ANCOVA, $F_{[2,11]} = 8.23$, $p < 0.01$; Tukey's HSD $p < 0.05$; Fig. 5*c*), and predators were more abundant in the CONTROL treatment (ANCOVA, $F_{[2,11]} = 7.15$, $p = 0.01$; Tukey's HSD $p < 0.05$; Fig. 5*e*). On both sampling dates, macroinvertebrate assemblages in each treatment were numerically dominated by *Paraleptophlebia* spp. (Ephemeroptera: Leptophlebiidae) and various chironomid taxa (Appendix A, Tables A1 and A2). There was an overall treatment effect on both invertebrate emergence rate (rmANOVA, $F_{[2,12]} = 10.15$, $p < 0.01$; Fig. 6*a*) and emergent biomass (rmANOVA, $F_{[2,12]} = 5.23$, $p = 0.02$; Fig. 6*b*) but no significant temporal trend between treatments for either variable (rmANOVA treatment × time, $p > 0.05$ for both).

Fish

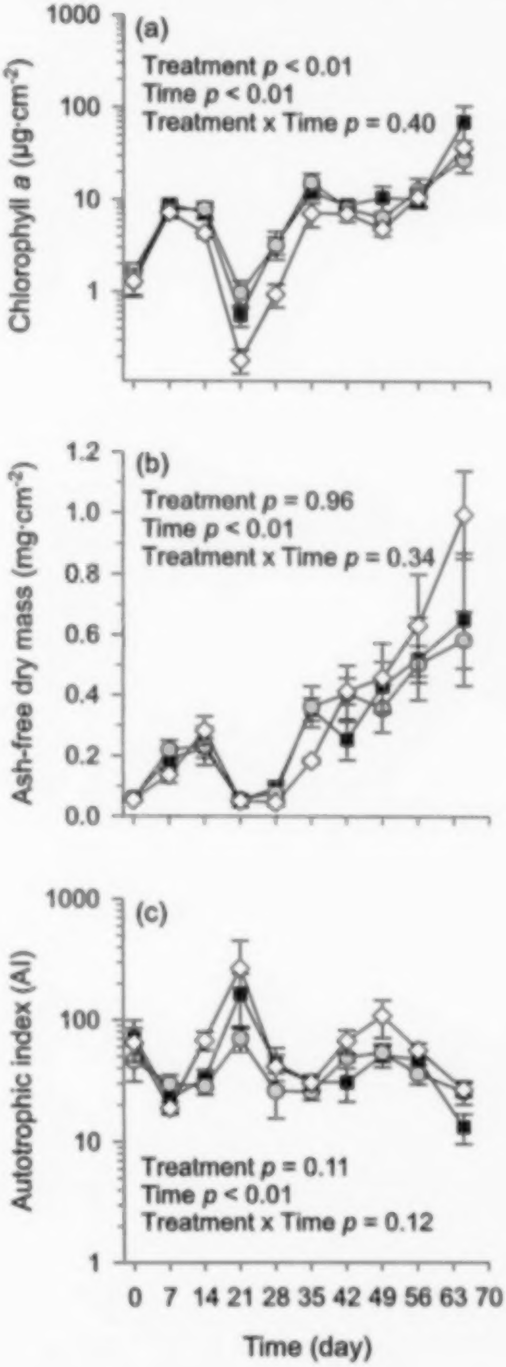
We found marked differences in age 0+ steelhead growth rates (ANOVA, $F_{[2,9]} = 30.40$, $p < 0.01$) and final condition factors (ANOVA, $F_{[2,9]} = 7.75$, $p < 0.01$) among treatments (Fig. 7). Mean condition factor (K) after 65 days was similar for fish reared in the NUTRIENT ($K = 1.05 \pm 0.01$) and CARCASS ($K = 1.07 \pm 0.01$) treatments but significantly higher than the mean K of fish in the CONTROL treatment ($K = 0.97 \pm 0.03$; Tukey's HSD, $p < 0.05$; Fig. 7*a*). While steelhead accumulated mass across all treatments, gains for each experimental group were significantly different from each other (Tukey's HSD, $p < 0.05$; Fig. 7*b*). Mean MSGRs were lowest for fish reared in the CONTROL treatment ($1.1 \pm 0.2\%\cdot g^{-1}\cdot day^{-1}$), intermediate in the NUTRIENT treatment ($1.9 \pm 0.1\%\cdot g^{-1}\cdot day^{-1}$), and greatest in the CARCASS treatment ($2.8 \pm 0.1\%\cdot g^{-1}\cdot day^{-1}$).

Discussion

In a recent meta-analysis of the SDN literature, Janetski et al. (2009) reported that responses of stream-resident fishes to salmon carcasses were generally stronger (i.e., exhibited a larger mean effect size) and more variable than those for most other food web constituents. Hypotheses for a positive response by juvenile salmonids to carcass inputs have included bottom-up flow of nutrients leading to increased periphyton and macroinvertebrate production (e.g., Kline et al. 1997; Gende et al. 2002) and the direct ingestion of salmon material (e.g., Wipfli et al. 2003; Giannico and Hinch 2007; Scheuerell et al. 2007). However, the contribution of these two alternative trophic pathways to juvenile salmonid production has been largely speculative, and this uncertainty has been identified as a critical knowledge gap in salmonid research (e.g., Gende et al. 2002; Wipfli et al. 2003; Janetski et al. 2009). We add to this discourse by providing a rigorous experimental assessment of the relative contribution of direct versus indirect pathways linking salmon carcasses to stream productivity across multiple trophic levels. Our study revealed that age 0+ steelhead trout reared in the presence of salmon carcass material exhibited significantly greater growth over 65 days relative to conspecifics reared in the presence of dissolved carcass leachate only or in carcass-free control enclosures. Although we did not directly examine stomach contents, steelhead in the CARCASS treatment were routinely observed consuming fragments of carcass flesh when such material was entrained in the water column. Hence, we attribute increased growth rates in the CARCASS treatment to the availability and utilization of carcass biomass.

Many previous SDN studies have been limited in scope to examinations of responses in stream water chemistry, indi-

Fig. 3. Time series of periphyton (*a*) chlorophyll *a* concentration, (*b*) ash-free dry mass, and (*c*) autotrophic index. Symbols represent mean values (±1 standard error, SE) for carcass (black squares), nutrient (gray circles), and control (open diamonds) treatment groups ($n = 5$ each). Probability (p) values were derived from repeated measures analysis of variance (rmANOVA).



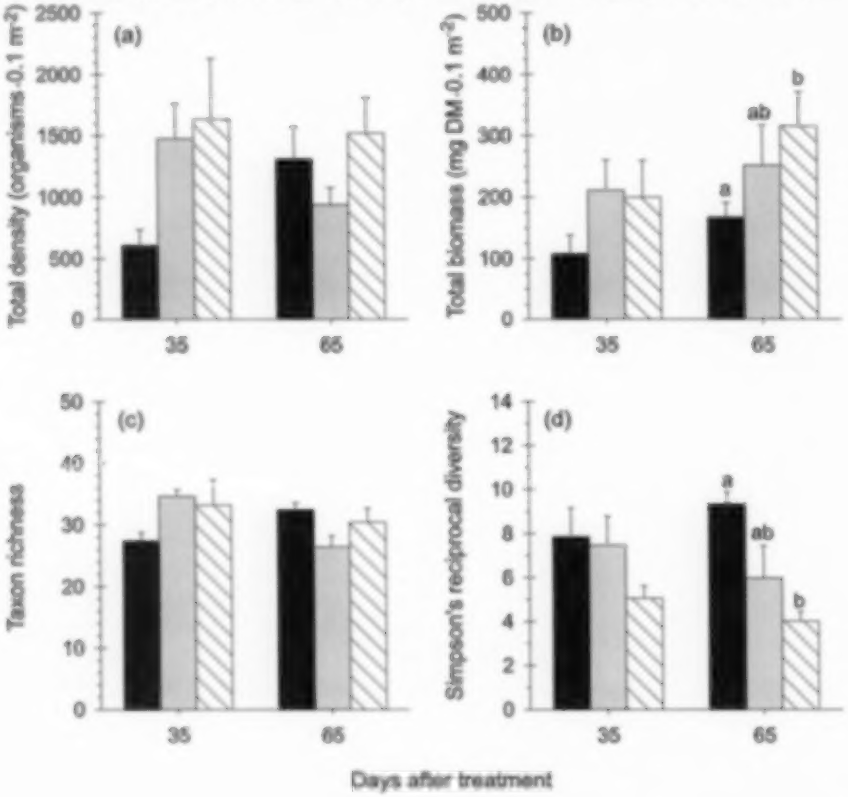
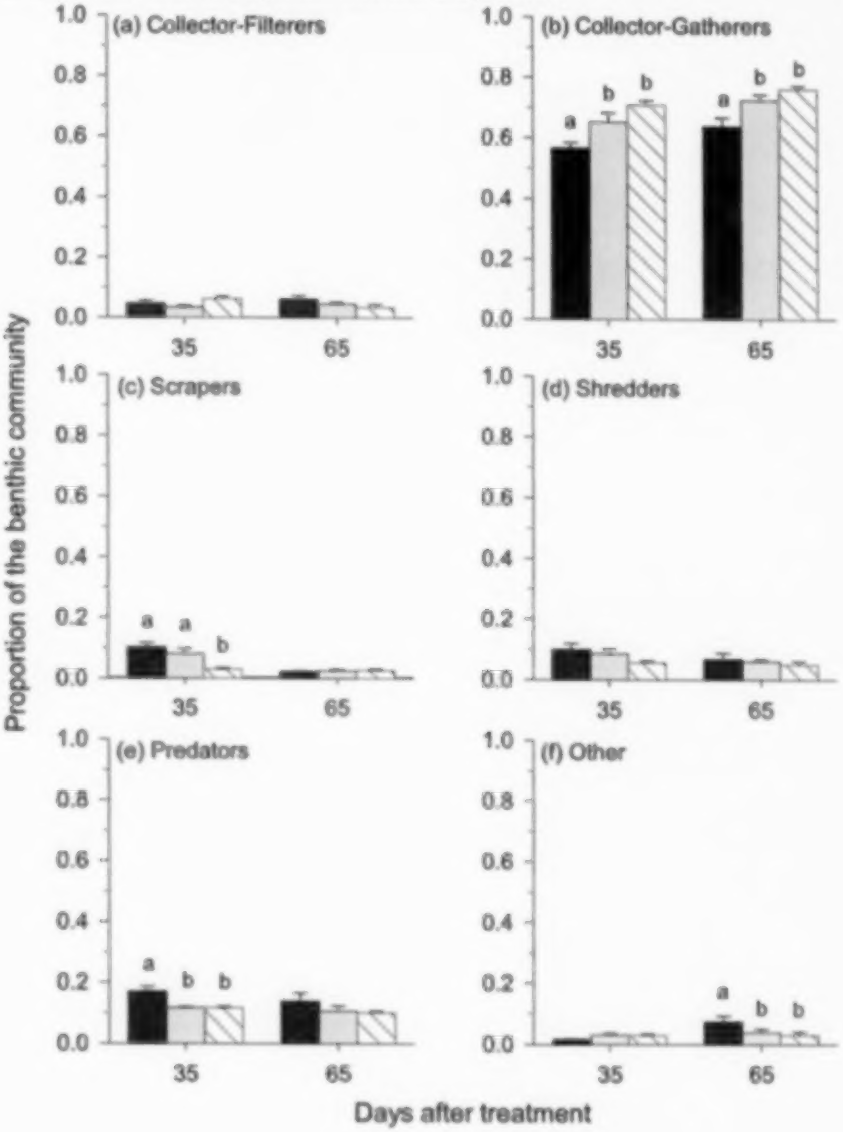


Fig. 4. Mean (+1 standard error, SE) benthic macroinvertebrate (*a*) total density, (*b*) biomass, (*c*) taxon richness, and (*d*) diversity for each treatment group after 35 and 65 days. Black, gray, and hatched bars represent control, nutrient, and carcass treatment groups, respectively ($n = 5$ each). Different lowercase letters above the bars indicate a statistically significant difference between treatments (analysis of variance (ANOVA) or analysis of covariance (ANCOVA) followed by Tukey's honestly significant difference test; $p < 0.05$).

ces of primary production, and one or two additional trophic levels (e.g., invertebrate primary and secondary consumers). The emergent paradigm from these works is that water chemistry variables, with the exception of dissolved organic carbon (see Janetski et al. 2009), generally exhibit a greater positive response to SDN inputs than freshwater biota (Chaloner et al. 2007). This discrepancy is often more pronounced in studies conducted in natural stream systems than in experimental mesocosms because of increased dissolved nutrient inputs via the excretion of metabolic waste products by live salmon. Additionally, the physical disruption of the streambed during redd construction may reduce standing stocks of periphyton and macroinvertebrates (Honea and Gara 2009). Nonetheless, in studies where biological responses are reported, they frequently occur at the base of the food chain (e.g., periphyton or epilithic biofilms) and then diminish at subsequent trophic levels (Chaloner et al. 2004). While our results for dissolved nutrients, periphyton, and macroinvertebrates were generally consistent with this trend, we found a marked biotic response among age 0+ steelhead trout, apex predators in our experimental food webs. Yearling steelhead exhibited substantial changes in growth and condition in response to SDN, even when carcass material was not directly available as a trophic resource. Collectively, our findings did not support the prediction that salmon carcass-derived leachate alone would result in increased productivity at all trophic levels, as neither periphyton AFDM nor the total biomass of benthic macroinvertebrates responded to the NUTRIENT treatment. Our second hypothesis (i.e., the availability of both carcass-derived leachate and material would result in greater productivity than leachate alone) was supported only for the growth of age 0+ steelhead trout over our 65-day experiment.

We observed two patterns with respect to the timing and duration of responses to SDN inputs. Treatment effects on dissolved NH_4^+ and periphyton Chl *a* were generally greatest between days 14 and 28 with little response thereafter. In contrast, increases in benthic and emergent invertebrate biomass lagged behind and did not manifest until some time after day 35 and were evident at the end of our 65-day experiment. Significant treatment effects on fish were also present at the end of the experiment. However, since we only assessed changes in fish growth and condition on day 65, we have no indication of when significant positive responses developed in each treatment. It is especially instructive to note that macroinvertebrate biomass and fish growth exhibited a tiered response to the two SDN treatments. By experiment's end, increases in invertebrate bio-

Fig. 5. Proportional contribution of different functional feeding groups (FFG) to the total macroinvertebrate assemblage in each treatment. Bars represent mean (+1 standard error, SE) proportional abundance in control (black), nutrient (gray), and carcass (hatched) treatment groups ($n = 5$ each). The "other" FFG designation includes omnivorous taxa and those for which reliable feeding guild information were unavailable. Different lowercase letters above the bars indicate a statistically significant difference between treatments (analysis of covariance (ANCOVA) followed by Tukey's honestly significant difference test; $p < 0.05$).



mass (both benthic and emergent) and fish growth for the CARCASS treatment were approximately twofold the increases observed for the NUTRIENT treatment.

Of the dissolved nutrients measured in our study, only NH_4^+ increased in response to carcass augmentation. Since northern California streams are typically nitrogen limited and have inherently low N:P ratios (Hill and Knight 1988), even modest increases in dissolved nitrogen may release periphyton from nutrient limitation and stimulate productivity. Empirical studies have shown that nitrogen limits periphyton growth at a N:P molar ratio <10:1 (Schanz and Juon 1983) and that a ratio of 16:1 is optimal for lotic primary production (Elwood et al. 1981). Despite elevated NH_4^+ concentrations in response to carcasses, such increases were of insufficient magnitude to increase mean dissolved N:P to values above 5:1 on any sample date apart from day 7, when mean N:P briefly spiked but remained <9:1 in all treatments. While there was an overall treatment effect on periphyton Chl *a* content, we found no evidence of a concomitant increase in periphyton biomass. However, our abil-

Fig. 6. Time series of aquatic invertebrate (*a*) emergence rate and (*b*) emergent biomass. Symbols represent the mean (±1 standard error, SE) of samples from carcass (black squares), nutrient (gray circles), and control (open diamonds) treatment groups (n = 5 each) at each time period. Probability (p) values were derived by repeated measures analysis of variance (rmANOVA).

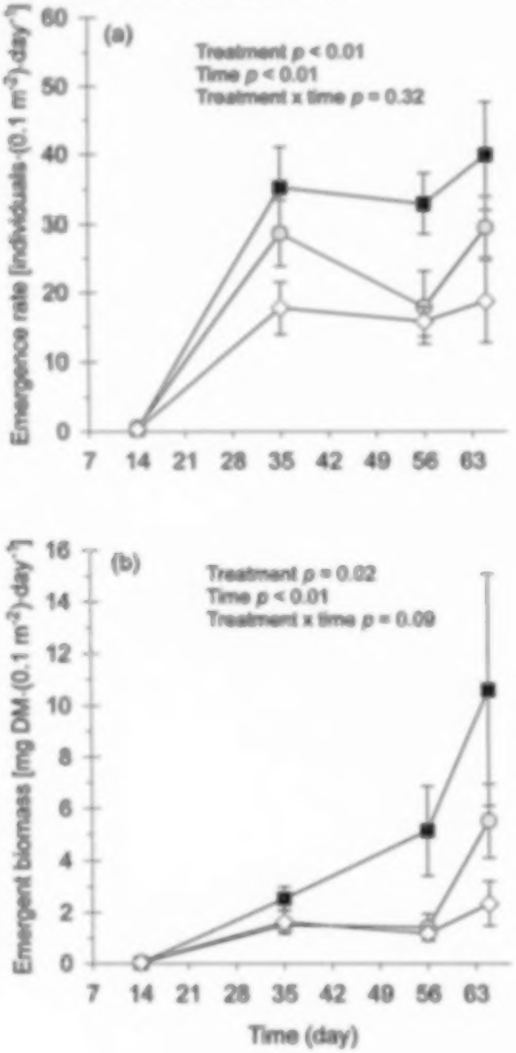
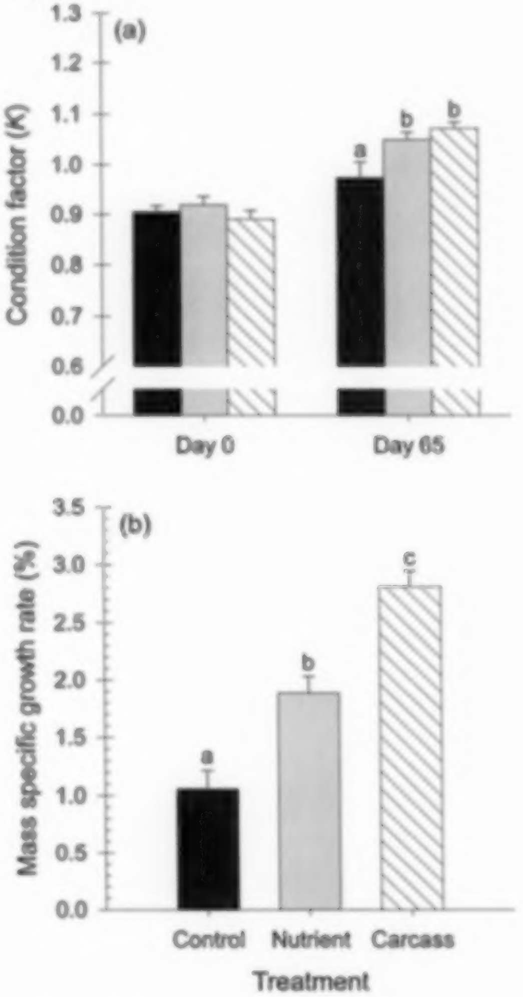


Fig. 7. (*a*) Pretreatment (day 0) and final (day 65) condition factors (mass per unit length) and (*b*) mass specific growth rates for age 0+ steelhead trout (*Oncorhynchus mykiss*) reared in each experimental treatment. Bars represent mean (+1 standard error, SE) values for control (black), nutrient (gray), and carcass (hatched) treatment groups. Different lowercase letters above bars indicate statistically significant differences between treatments (analysis of variance (ANOVA) followed by Tukey's honestly significant difference test; $p < 0.05$).



ity to detect an overall effect of SDN on periphyton biomass may have been influenced by increased macroinvertebrate grazing and biomass removal in the two carcass augmented treatments.

On balance, the benthic macroinvertebrate community was only moderately influenced by the addition of SDN subsidies. Densities of most individual taxa were largely unaffected or exhibited very modest increases in response to carcass augmentation. After 35 days, only leptophlebiid mayflies (*Paraleptophlebia* spp.) and chironomids appeared to respond positively to SDN subsidies. Increases in the abundance or biomass of chironomid and mayfly taxa have been observed in many stream fertilization experiments (e.g., Pearson and Connolly 2000; Ramírez and Pringle 2006), presumably because of their short generation times and high colonization capacity (Rosser and Pearson 1995). At experiment's end, only the density of *Paraleptophlebia* in the CARCASS treatment was significantly higher (after Bonferroni–Holm correction), whereas chironomids generally decreased in the NUTRIENT and CARCASS treatments relative to densities at day 35, but increased in CONTROL enclosures. While the higher proportion of collector–gatherers observed in CARCASS treatment may be partially explained by the availability of carcass fragments, it is unclear what organic matter source was supporting higher proportions of this FFG in the NUTRIENT treatment. One possible explanation is that the external surface of the Nitex bags (containing the carcass sections) developed a substantial microbial coating around day 21. Following elevated streamflow on day 37, large portions of the microbial layer began sloughing from the surface of the bags. Although the bulk of this material was entrained and immediately transported out of each enclosure, small fragments were occasionally observed on the streambed and in interstitial spaces. This flocculate material may have served as an important carbon source for collector–gatherers in the NUTRIENT treatment and contributed to their increased proportional abundance.

It is important to recognize that the short duration of most SDN studies, including our own, provides limited information on the true dynamics of macroinvertebrate populations. Short-term studies are frequently biased towards finding significant responses in small-bodied, multivoltine invertebrate taxa such as chironomids. Though statistically significant differences in total macroinvertebrate density were not observed in our study, trends in diversity and total biomass suggest subtle but important differences in invertebrate production among treatments. One notable result from our macroinvertebrate sampling was the high density of chironomid pupae in both NUTRIENT and CARCASS treatments on day 35 and again in the CARCASS treatment on day 65. High numbers of pupating organisms, together with higher emergence rates from the same treatments, suggest the effects of salmon carcasses on secondary production may be appreciably greater than density and biomass estimates indicate. Benthic samples collected at monthly intervals simply provide a snapshot of community composition and offer little information concerning how SDN subsidies affect the annual production and biomass turnover of stream invertebrates. Such information is largely unknown (but see Lessard et al. 2009) and would greatly improve our understanding of the linkages that exist between salmon carcasses and the production of juvenile salmon.

We acknowledge a number of potentially confounding issues associated with our study design. First, our carcass loading rate translated to ~3.0 kg·m^{-2} on an areal basis and was higher than those reported in many previous studies (e.g., Wipfli et al. 2003; Wilzbach et al. 2005; but see Johnston et al. 1997). We selected this rate after a pilot study conducted the previous year revealed that the much of the carcass material was entrained and deposited downstream of our small (0.74 m^2) experimental enclosures making it effectively unavailable to the confined biota. While this loading rate would be unrealistic over most spatial scales, carcasses tend to be patchily distributed in the Navarro River watershed and can accumulate at relatively high densities (2–3 carcasses·m^{-2}) in localized areas where resident fish rear (J.D. Kiernan, personal observation). Second, the timing of our experiment was delayed relative to the natural timing of coho spawning in northern California streams. We initiated our study in spring rather than winter to minimize potential flood damage to our experimental units and so that age 0+ steelhead trout could be used as a proxy for juvenile coho salmon, which are protected under the US Endangered Species Act. Although coho salmon carcasses are not present in the Navarro watershed during spring, spawning steelhead trout presumably transfer marine nutrients and biomass during this period. Finally, the restricted temporal and spatial scales of our study limit our ability to generalize to scales (e.g., reach-level spatial and yearly or greater temporal) that are relevant to salmonid production. Clearly, results obtained in our experimental enclosures demonstrate potential responses by stream biota but may not accurately mimic processes occurring in natural stream communities. Despite these limitations, we believe our findings provide a novel perspective on the importance of salmon carcasses to lotic food webs.

It is widely believed that diminished wild salmon populations have caused a corresponding decrease in the amount of nutrients and organic matter being delivered to many Pacific Rim ecosystems today (Gresh et al. 2000; Naiman et al. 2002). Consequently, the deployment of salmon carcasses, carcass analogues, and inorganic nutrients to mitigate for the loss of SDN to spawning and rearing habitats is becoming increasingly commonplace (Lackey 2003). Our study provides insight into the key pathways by which salmon-derived nutrients and biomass influence freshwater productivity that may be used to develop effective restoration tools and strategies. We demonstrate that while nutrients released during salmon carcass decomposition enhance the short-term growth and condition of juvenile salmonids via bottom-up trophic pathways, the direct consumption of carcass biomass such as fragments of flesh promotes a significant amount of additional growth. This implies that efforts to increase the productivity of salmon-bearing streams through the addition of inorganic fertilizers may not be as effective as the application of surplus carcasses or manufactured carcass analogues, which closely mimic the biochemical and physical composition of salmon carcasses. Further, data from our study suggest that resource managers should seek to ensure long-term retention of salmon carcasses within the aquatic ecosystem.

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Appendix A

Appendix tables appear on following pages.

Table A1. Mean (±1 standard error, SE) densities of select macroinvertebrate taxa in each treatment group at 35 days after treatment.

		Treatment group			ANOVA	
Taxon	FFG	Control	Nutrient	Carcass	*F*	*p*
Ephemeroptera						
Baetidae						
Centroptilum–Procloeon sp.	CG	7±3	17±5	38±14	2.33	0.139
Heptageniidae						
Nixe sp.	SC	57±15	53±17	25±8	2.77	0.103
Leptophlebiidae						
Paraleptophlebia spp.	CG	199±49	502±96	685±207	4.34	0.038
Plecoptera						
Chloroperlidae (nondistinct)	P	11±5	10±4	9±4	NT	NT
Nemouridae						
Malenka sp.	SH	11±3	6±1	11±4	1.06	0.378
Perlidae						
Calineuria californica	P	24±7	19±7	12±3	1.37	0.292
Megaloptera						
Sialidae						
Sialis sp.	P	43±17	84±20	95±29	1.86	0.197
Trichoptera						
Lepidostomatidae						
Lepidostoma sp.	SH	19±6	36±17	41±14	0.80	0.471
Diptera						
Chironomidae (nondistinct)	Various	3±2	22±8	25±15	NT	NT
Chironomidae (pupae)	Various	10±2a	61±7b	32±7b	19.85	**<0.001**
Orthocladiinae						
Brillia sp.	SH	28±12	69±32	22±8	1.62	0.239
Corynoneura sp.	CG	25±2	104±18	130±58	3.67	0.057
Parametriocnemus sp.	CG	16±8	8±3	15±4	0.15	0.865
Rheocricotopus sp.	OM	9±2	48±23	36±13	4.54	0.034
Synorthocladius sp.	CG	6±2	30±9	31±12	4.37	0.037
Chironominae						
Chironomini						
Microtendipes sp.	CF	9±5	17±4	54±18	4.84	0.029
Phaenopsectra sp.	SC	4±4	65±42	14±7	6.46	0.012
Polypedilum sp.	CG	20±4	46±16	25±9	0.81	0.467
Tanytarsini						
Micropsectra–Tanytarsus sp.	CG	15±7	65±33	102±51	2.67	0.110
Paratanytarsus sp.	CF	3±1	14±6	32±12	3.06	0.084
Stempellinella sp.	CF	20±7	19±2	13±2	0.59	0.567
Tanypodinae						
Pentaneurini						
Paramerina sp.	P	7±3	29±3	38±15	4.39	0.037
Oligochaeta	CG	11±4	24±7	19±8	1.02	0.390

Note: Density values represent the number of individuals per 0.1 m^2. Included are taxa that compose ≥2% of the total benthic assemblage for at least one treatment. Functional feeding group (FFG) abbreviations are collector–gatherers (CG), collector–filterers (CF), scrapers (SC), shredders (SH), predators (P), and omnivores (OM). *p* values in bold indicate a statistically significant difference after Bonferroni–Holm (step-down) correction (analysis of variance (ANOVA), *df* = 2, 12). Different letters indicate treatments that were significantly different according to Tukey's honestly significant difference (HSD) (treatments sharing the same letter are not different). Nondistinct taxa were not tested (NT) statistically.

Table A2. Mean (±1 standard error, SE) densities of select macroinvertebrate taxa in each treatment group at the end of the 65 day experiment.

		Treatment group			ANOVA	
Taxon	FFG	Control	Nutrient	Carcass	*F*	*p*
Ephemeroptera						
Baetidae						
Centroptilum–Procloeon sp.	CG	51±20	35±11	60±16	0.51	0.615
Heptageniidae						
Nixe sp.	SC	15±5	15±4	27±4	2.37	0.136
Leptophlebiidae						
Paraleptophlebia spp.	CG	310±57a	360±49a	712±99b	8.48	**0.002**
Megaloptera						
Sialidae						
Sialis sp.	P	34±5	20±5	34±9	1.77	0.219
Trichoptera						
Lepidostomatidae						
Lepidostoma sp.	SH	58±18	41±5	59±15	0.50	0.620
Diptera						
Chironomidae (nondistinct)	Various	23±8	10±5	15±6	NT	NT
Chironomidae (pupae)	Various	11±3	17±5	37±9	4.41	0.037
Orthocladiinae						
Corynoneura sp.	CG	44±14	27±12	25±10	3.67	0.057
Heterotrissocladius sp.	CG	20±7	10±3	12±5	0.89	0.435
Psectrocladius sp.	CG	128±44	52±22	72±43	0.22	0.802
Rheocricotopus sp.	OM	88±25	36±15	48±21	1.17	0.344
Chironominae						
Chironomini						
Polypedilum sp.	CG	20±12	15±5	27±21	0.14	0.872
Tanytarsini						
Micropsectra–Tanytarsus sp.	CG	156±46	76±23	101±37	1.19	0.337
Paratanytarsus sp.	CF	61±24	28±10	32±16	0.88	0.440
Tanypodinae						
Pentaneurini						
Ablabesmyia sp.	CG	22±9	7±2	14±3	2.05	0.171
Paramerina sp.	P	72±12	41±7	78±20	2.24	0.149
Thienemannimyia group	P	20±8	10±4	11±6	0.93	0.420
Oligochaeta	CG	15±8	44±25	31±15	0.50	0.620

Note: Density values represent the number of individuals per 0.1 m^2. Included are taxa that compose ≥2% of the total benthic assemblage for at least one treatment. Functional feeding group (FFG) abbreviations are collector–gatherers (CG), collector–filterers (CF), scrapers (SC), shredders (SH), predators (P), and omnivores (OM). *p* values in bold indicate a statistically significant difference after Bonferroni–Holm (step-down) correction (analysis of variance (ANOVA), *df* = 2, 12). Different letters indicate treatments that were significantly different according to Tukey's honestly significant difference (HSD) (treatments sharing the same letter are not different). Nondistinct taxa were not tested (NT) statistically.

Evidence of farm-induced parasite infestations on wild juvenile salmon in multiple regions of coastal British Columbia, Canada

M.H.H. Price, A. Morton, and J.D. Reynolds

Abstract: Salmon farms are spatially concentrated reservoirs of fish host populations that can disrupt natural salmonid host–parasite dynamics. Sea lice frequently infect farm salmon and parasitize sympatric wild juvenile salmonids, with negative impacts on survival in Europe and Pacific Canada. We examined louse parasitism of wild juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) from three salmon farming regions in British Columbia (Finlayson, Broughton Archipelago, and Georgia Strait). We compared sites of low and high exposure to farms and included an area without farms (Bella Bella) to assess baseline infection levels. Louse prevalence and abundance were lowest and most similar to natural baseline levels at low-exposure sites and highest at high-exposure sites in all farm regions. A significantly greater proportion of the lice were *Lepeophtheirus salmonis* at high-exposure sites. Exposure to salmon farms was the only consistently significant factor to explain the variation in prevalence data, with a secondary role played by salinity. Our results support the hypothesis that salmon farms are a major source of sea lice on juvenile wild salmon in salmon farming regions and underscore the importance of using management techniques that mitigate threats to wild stocks.

Résumé : Les élevages de saumons sont des réservoirs concentrés dans l'espace de populations de poissons hôtes qui peuvent perturber la dynamique naturelle des saumons hôtes et de leurs parasites. Les puces de mer infectent fréquemment les saumons d'élevage et parasitent les jeunes salmonidés sauvages sympatriques, ce qui a des impacts négatifs sur la survie en Europe et la région pacifique du Canada. Nous avons étudié le parasitisme par les puces de mer chez les saumons kéta (*Oncorhynchus keta*) et roses (*Oncorhynchus gorbuscha*) dans trois régions d'élevage de saumons en Colombie-Britannique (Finlayson, archipel de Broughton et détroit de Géorgie). Nous avons comparé les sites fortement et faiblement exposés aux élevages, ainsi qu'une région sans élevages (Bella Bella), afin d'évaluer les niveaux d'infection de base. La prévalence et l'abondance des puces de mer sont minimales et le plus semblables aux niveaux de base naturels aux sites de faible exposition, et maximales aux sites de forte exposition dans toutes les régions d'élevage. Aux sites de forte exposition, une proportion significativement plus élevée des puces de mer appartient à l'espèce *Lepeophtheirus salmonis*. L'exposition aux élevages de saumons est le seul facteur explicatif constamment significatif dans les données de prévalence avec la salinité qui joue un rôle secondaire. Nos résultats appuient l'hypothèse selon laquelle les élevages de saumons sont une source importante de puces de mer pour les jeunes saumons sauvages dans les régions d'élevage de saumons et ils soulignent l'importance d'utiliser des techniques de gestion qui réduisent les menaces aux stocks sauvages.

[Traduit par la Rédaction]

Introduction

Disease outbreaks are an increasing threat to wildlife, exacerbated by increases in the human population and domesticated animals (Macdonald and Laurenson 2006; Thirgood 2009). The most common route of transmission to wildlife is from artificial reservoirs of host populations (McCallum and Dobson 1995; Daszak et al. 2000). Marine salmon farms located along near-shore wild salmon migration routes provide spatially concentrated host populations that can serve as reservoirs and perturb the dynamics of natural salmonid host–parasite systems (Krkošek et al. 2006, 2010; Costello 2009). Sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.) frequently infect farm salmon, and many studies in Europe have identified farm-origin lice as those that parasitize sympatric wild salmonids (MacKenzie et al. 1998; Tully et al. 1999; Bjorn and Finstad 2002). Moreover, parasite outbreaks from salmon farms have been implicated in the collapse of wild sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) populations in Norway, Scotland, and Ireland (McVicar 1997, 2004).

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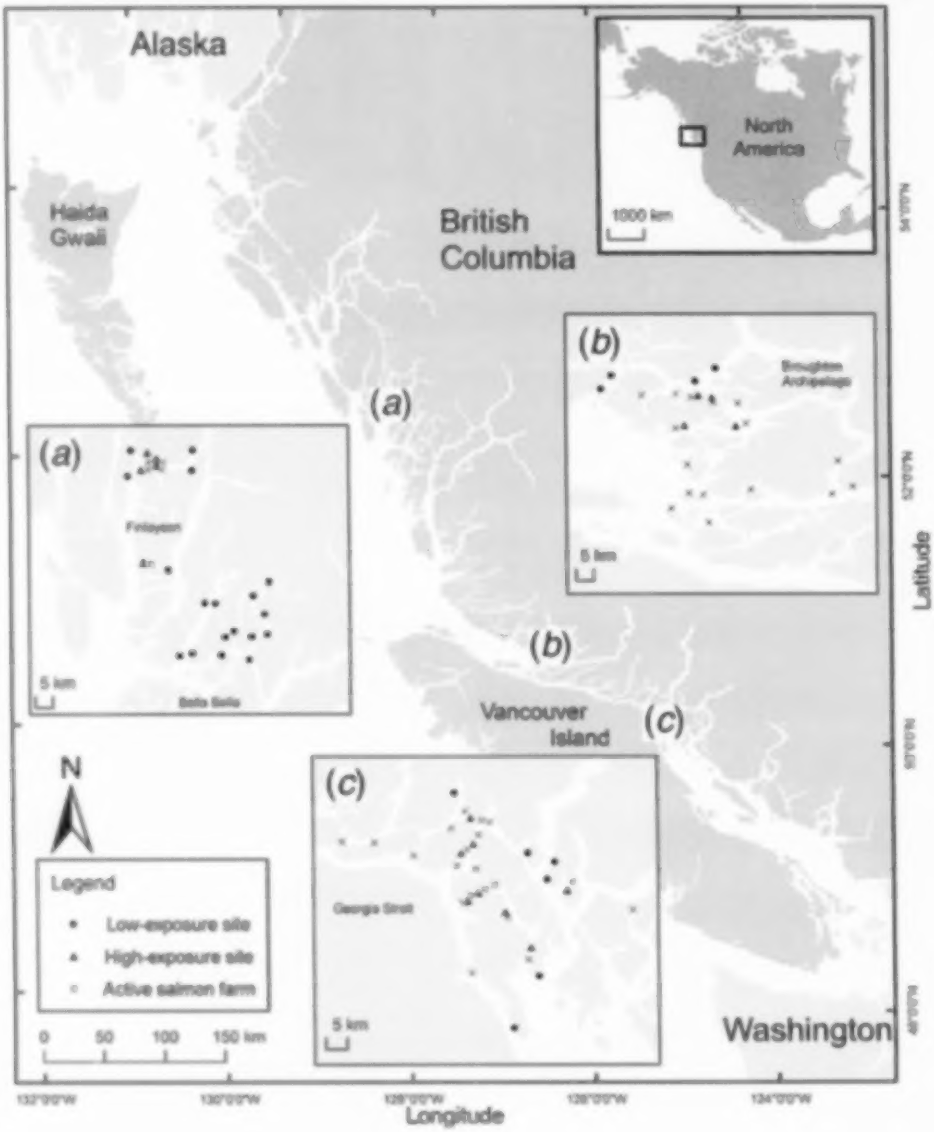
Fig. 1. Study area, including three salmon farm regions (*a*–*c*), the non-salmon farm area of Bella Bella, and all associated sampling sites for juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined for sea lice in British Columbia, Canada, in 2007 and 2008.


Alaska
Haida Gwaii
British Columbia
North America
1000 km
(a)
(b)
(c)
Finlayson
Bella Bella
5 km
Broughton Archipelago
Vancouver Island
Georgia Strait
Washington
N
Legend
Low-exposure site
High-exposure site
Active salmon farm
0 50 100 150 km
132°0'0"W
130°0'0"W
128°0'0"W
126°0'0"W
124°0'0"W
Longitude
54°0'0"N
52°0'0"N
50°0'0"N
48°0'0"N
Latitude

In Pacific Canada, recurrent parasite infestations transmitted from farms to wild juvenile pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) have been well documented in the Broughton Archipelago (Krkošek et al. 2005*a*, 2006; see our Fig. 1), where the first epizootic in British Columbia was observed (Morton and Williams 2003). Pink salmon populations have shown a general decline in this region, and there is evidence that farm-origin lice may be partly responsible (Pacific Fisheries Resource Conservation Council 2002; Krkošek 2007*a*; Ford and Myers 2008). Additionally, a recent investigation has shown parasite outbreaks on wild salmon in a salmon farm region south of the Broughton, in nearby Georgia Strait (Morton et al. 2008). Given the current intensity of farmed salmon produced in British Columbia, and the proposed expansion of the industry, there is concern that lice outbreaks and negative impacts on wild salmon populations could occur elsewhere.

Alternative explanations have been suggested for the origins of sea lice on wild juvenile salmon in fish farming regions (Brooks 2005; Beamish et al. 2007; Jones and Hargreaves 2007). Factors such as temperature, salinity, and presence and abundance of wild fish hosts have been cited. Adding to this uncertainty is a paucity of information on lice

Table 1. Summary of mean capture site and biological data values for juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined in coastal British Columbia in 2007 and 2008.

Location	Exposure	Salinity (‰)	Temperature (°C)	Species	Fork length (cm)*	Mass (g)*
Bella Bella	Low	20.1	10.6	Chum	4.79 (0.02)	1.28 (0.02)
				Pink	4.68 (0.03)	1.21 (0.04)
Finlayson	Low	25.2	9.4	Chum	4.75 (0.05)	0.70 (0.00)
				Pink	4.34 (0.03)	1.20 (0.16)
	High	26.3	9.5	Chum	5.23 (0.07)	2.27 (0.22)
				Pink	4.80 (0.05)	1.18 (0.10)
Broughton Archipelago	Low	27.6	10.4	Chum	4.19 (0.17)	—
				Pink	3.76 (0.24)	—
	High	21.5	9.5	Chum	4.48 (0.31)	—
				Pink	3.92 (0.26)	—
Georgia Strait	Low	24.9	10.4	Chum	5.41 (0.45)	2.19 (0.08)
				Pink	5.87 (0.76)	2.54 (0.17)
	High	27.6	12.1	Chum	5.93 (0.39)	2.71 (0.08)
				Pink	5.61 (0.67)	2.19 (0.07)

*Standard error is in parentheses.

Table 2. Mean prevalence (P), abundance (A), and intensity (I) of sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*) on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined in 2007 and 2008 among four coastal regions of British Columbia and exposure (low or high) of these wild fish species to salmon farms.

Location	Year	Exposure	No. of fish	*L. salmonis*			*C. clemensi*			Combined prevalence*	Combined abundance
				P	A	I	P	A	I		
Chum											
Bella Bella	2007	Low	1504	2.1	0.0	1.0	2.2	0.0	1.1	4.2	0.0
	2008	Low	1916	0.5	0.0	1.0	2.5	0.0	1.0	2.9	0.0
Finlayson	2008	Low	317	0.0	0.0	0.0	1.3	0.0	1.0	1.3	0.0
		High	372	3.2	0.1	2.0	16.1	0.2	1.0	19.1	0.3
Broughton Archipelago	2007	Low	910	0.5	0.0	1.0	1.3	0.0	1.2	1.8	0.0
		High	717	13.5	0.2	1.2	15.1	0.2	1.4	25.9	0.4
Georgia Strait	2007	Low	674	15.6	0.2	1.4	19.9	0.3	1.4	29.8	0.5
	2008	Low	169	7.1	0.1	1.3	10.1	0.1	1.4	15.4	0.2
	2007	High	884	18.4	0.3	1.6	24.8	0.3	1.4	37.3	0.6
	2008	High	635	23.6	0.6	2.4	17.2	0.4	1.9	37.2	1.0
Pink											
Bella Bella	2007	Low	479	1.3	0.0	1.0	2.3	0.0	1.1	3.5	0.0
	2008	Low	955	0.4	0.0	1.0	2.7	0.0	1.0	3.1	0.0
Finlayson	2008	Low	774	0.3	0.0	1.0	4.3	0.0	1.0	4.5	0.0
		High	741	3.5	0.1	4.6	14.7	0.2	1.0	18.5	0.2
Broughton Archipelago	2007	Low	473	0.8	0.0	1.0	0.2	0.0	1.0	0.8	0.0
		High	697	20.4	0.2	1.2	24.2	0.4	1.5	37.7	0.6
Georgia Strait	2007	Low	82	20.7	0.3	1.3	15.9	0.2	1.5	32.9	0.5
	2008	Low	79	8.8	0.1	1.1	11.4	0.1	1.1	19.0	0.2
	2007	High	538	37.4	0.7	1.8	20.3	0.3	1.4	48.9	1.0
	2008	High	510	12.7	0.2	1.4	18.0	0.3	1.7	27.3	0.5

*Combined prevalence includes *L. salmonis*, *C. clemensi*, and unidentified chalimus A and B stages.

levels in farm regions beyond the Broughton Archipelago. Additionally, there is a lack of information on lice levels in regions without salmon farms, which could be compared with concurrent data gathered in active farm regions. Moreover, no investigation has examined the relationship between lice levels on wild juveniles and the total amount of salmon produced on farms in a region.

In this study we examine multiple potential causes and correlates of lice infections on juvenile chum and pink salmon from four regions in British Columbia. We extend our comparative investigation beyond the Broughton Archipelago to include Bella Bella (an area without salmon farms) and the salmon farming regions of Finlayson to the north and Georgia Strait to the south.

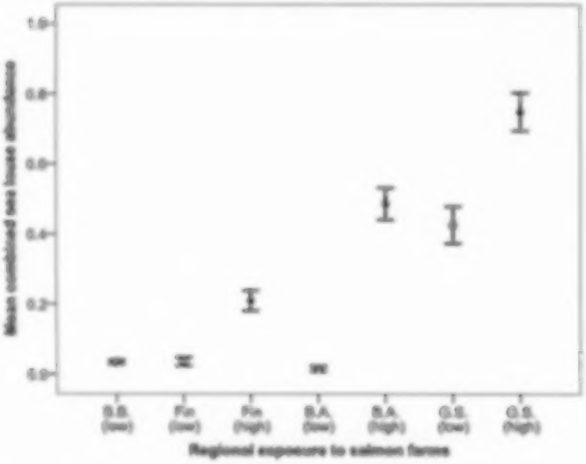


Fig. 2. The 95% confidence intervals of combined mean sea louse (*Lepeophtheirus salmonis* and *Caligus clemensi*) abundance on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined at sites of low (open circle) or high (filled circle) exposure to salmon farms for all years combined. B.B., Bella Bella; Fin, Finlayson; B.A., Broughton Archipelago; G.S., Georgia Strait.

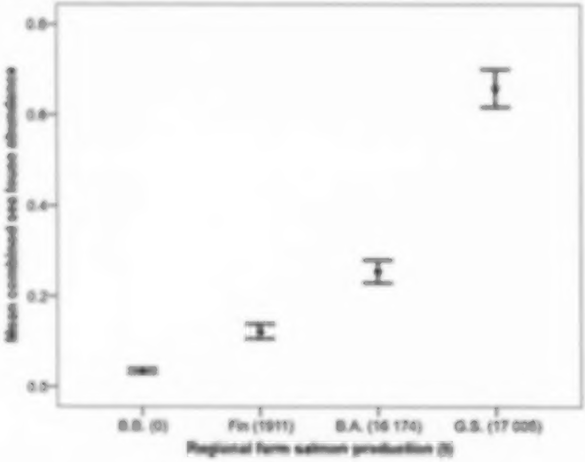


Fig. 3. The 95% confidence intervals of combined mean sea louse (*Lepeophtheirus salmonis* and *Caligus clemensi*) abundance on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined among four areas of coastal British Columbia and their associated farm salmon production in tonnes (t). B.B., Bella Bella; Fin, Finlayson; B.A., Broughton Archipelago; G.S., Georgia Strait.

Materials and methods

We collected early marine phase juvenile chum and pink salmon from four regions along the British Columbia coast from March to June 2007 and 2008 (Fig. 1). Capture locations were selected based on the probability of exposure of juvenile salmon to active salmon farms, categorized as high (<1 km from active farms) or low (4–40 km upstream from farms; Fig. 1). Some low-exposure sites were relatively near an active salmon farm (4 km). However, these sites were situated along migration corridors upstream of the predominant flow from farms or across large channels that juveniles at the time of capture are known not to cross. Thus, we considered the exposure probability at those sites to be low. This way of categorizing exposure matches that in similar studies within the Broughton Archipelago and Georgia Strait (Morton et al. 2004, 2005, 2008). It would not have been appropriate to treat probability of exposure as a continuous variable based on distance from the nearest farm, because that would have ignored the movements of fish from upstream (pre-exposure) to downstream (post-exposure) of farms. We determined the activity status of farms (i.e., active or fallow) and annual production harvest during the years of study from the Oceans and Marine Fisheries Branch of the British Columbia Ministry of Environment (British Columbia Ministry of the Environment 2009; Fig. 1). Sites near farms that were fallow in a given year were considered low exposure. Dates and frequency of surveys varied slightly between regions: Finlayson, 23 April – 22 June (biweekly); Bella Bella, 17 April – 15 June (weekly); Broughton Archipelago, 20 March – 15 May (biweekly); Georgia Strait, 22 April – 14 June (biweekly).

At each site, juveniles were corralled by beach seine (50 m long, 6 mm mesh) from a boat, and in all regions except Georgia Strait, subsets of 30–100 juveniles per site were haphazardly selected and live-sampled for sea lice using methodology described by Krkošek et al. (2005*b*). Because this technique broadly categorizes chalimus stages of lice into only two stages and not acccording to species, we modified this approach in Finlayson and Bella Bella by euthanizing and collecting only those juvenile salmon that hosted a louse. All infected juveniles were frozen and sent to a lab for louse and host species identification, as well as fork length and mass measurements, as described by Morton et al. (2008). To assess observer accuracy during nonlethal sampling, we also euthanized three juveniles per sampling day in Finlayson and Bella Bella ($n = 100$) that were judged to be louse-free and later assessed them for louse presence using a dissecting microscope; no fish had lice. Only adult and copepodid stages of sea lice were identified in the Broughton Archipelago (for reasons explained above; but all lice were counted), and fish species and fork length were recorded without taking mass measurements according to nonlethal field assessment methods (Krkošek et al. 2005*b*). In Georgia Strait, entire subsets of juveniles (30–50 per site per week) were euthanized and lethally assayed for sea lice as described above. We recorded sea surface salinity and temperature at each collection site per sampling event among all regions using a calibrated YSI 85 multifunction meter (YSI Inc., Yellow Springs, Ohio). Measures of lice infection rates are as follows: prevalence is the number of hosts infected with lice (expressed as a percentage), abundance is the total number of lice divided by the total number of hosts (infected and uninfected), and intensity is the mean number of lice per infected host (Margolis et al. 1982).

We were interested in which factors most influence sea louse infection levels on juvenile salmon in British Columbia. Accordingly, based on the literature cited in the Introduction, we formulated a priori hypotheses relating fish capture sites to the prevalence of sea lice on juveniles cap-

Table 3. Percentages of sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*) at different life stages infecting juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined among three coastal regions of British Columbia and exposure (low or high) of these wild fish species to salmon farms.

		L. salmonis						*C. clemensi*				
Location	Exposure	No. of lice	Copepodid (%)	Chalimus A (%)	Chalimus B (%)	Preadult (%)	Adult (%)	No. of lice	Copepodid (%)	Chalimus A (%)	Chalimus B (%)	Adult (%)
Bella Bella	Low	68	8.3	33.3	16.7	8.3	33.3	135	12.8	53.2	17.0	17.0
Finlayson	Low	2	0.0	0.0	33.3	33.3	33.3	38	17.4	65.2	8.7	8.7
	High	61	23.5	48.2	14.1	7.1	7.1	171	11.6	44.2	11.6	32.6
Georgia Strait	Low	189	10.2	37.1	18.4	14.7	19.6	236	10.2	47.6	28.2	14.0
	High	1046	8.0	38.7	20.0	17.0	16.2	840	8.0	38.9	30.8	22.3

Note: Broughton Archipelago is not included because of unidentified species in chalimus stages during live sampling.

tured at those sites. Specifically, we hypothesized that fish from locations that were more exposed to farms would have higher louse prevalence and that high temperature and salinity would also be correlated with high lice loads (because sea louse growth in lab-based trials depends strongly on temperature and salinity; Pike and Wadsworth 1999; Costello 2006).

We used linear mixed-effects modelling to account for the hierarchical nature of the sampling, where multiple sampling events at a given location were treated as random factors nested within location, which itself was a random factor nested within a region. We included exposure category (low or high) nested within region, temperature, salinity, and fork length as fixed factors to examine their influence on sea louse infection levels on juvenile salmon. Our initial model selection included analyses for each louse and host species, respectively; however, because results were broadly similar for each analysis, we combined louse prevalence and host species for simplification of presentation (minor differences are discussed in the Results). Thus, for the model, we averaged prevalence for combined sea louse species (*L. salmonis* and *Caligus clemensi*) for all host individuals (pink and chum) within a sampling event (i.e., replicate; $n = 296$) and transformed prevalence data using an arcsine square-root function to correct for unequal variances and nonnormality. We tested a set of candidate models using Akaike's information criterion (AIC) and then evaluated ΔAIC to select the best approximating model(s). We made appropriate inference using $\Delta\text{AIC} < 4$ to describe the top model set. Finally, we summed Akaike weights (ω_i) across the top model set for each variable to rank them by importance (Burnham and Anderson 1998; Anderson et al. 2001).

We performed a χ^2 test to examine whether the ratio of louse species abundances changed in accordance to a given salmon farm region and associated differences in farm salmon production. We performed all statistical tests using SPSS 16.0 for Mac (SPSS 2007).

Results

We assessed a total of 13 426 juvenile chum and pink salmon over 296 sampling episodes for sea louse parasitism across the four regions in 2007 and 2008. Juvenile salmon were largest in Georgia Strait and smallest in the Broughton Archipelago, and both pink and chum salmon were larger, on average, at high-exposure sites in all farm regions except pink salmon in Georgia Strait, where they were larger at low-exposure sites (Table 1). Sea surface salinity and temperature were higher on average at sites of high exposure than at sites of low exposure.

Louse prevalence and abundance were lowest for both chum and pink salmon in all farm regions at sites of low exposure and most similar to Bella Bella, where there are no farms (Table 2; Fig. 2). In a comparison among the four regions, combined louse abundance was highest in Georgia Strait, where salmon production is greatest (Fig. 3). Increases in combined louse abundance between sites of low and high exposure ranged from a 2.4-fold increase at Georgia Strait, to a 7.1-fold increase at Finlayson, to a 30.5-fold increase in the Broughton Archipelago. A greater proportion of the lice were *L. salmonis* at sites of high exposure (χ^2 =

Table 4. List of candidate models and resulting Akaike's information criterion (AIC) scores used to determine which factors most influence sea louse prevalence on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*).

Model	*K*	AIC	ΔAIC	ω_i
Exposure + salinity*	4	–255.069	0.000	0.394
Exposure*	3	–254.660	0.409	0.321
Exposure + temperature*	4	–254.231	0.838	0.259
Exposure + length	4	–248.094	6.975	0.012
Length	3	–221.4	33.674	0.000
Salinity	3	–213.52	41.551	0.000
Temperature	3	–212.54	42.535	0.000
Salinity + temperature	4	–205.107	49.962	0.000
Salinity + temperature + (salinity × temperature)	5	–194.39	60.680	0.000

Note: Model structure, number of parameters + intercept + covariance structure (*K*), AIC, ΔAIC, and Akaike weight (ω_i) are included; exposure is fish exposure to farms (low or high), salinity is sea surface salinity, temperature is sea surface temperature, and length is host fork length.

*A model of the top model set.

3.814, df = 1, $p \leq 0.001$), and lice at all locations were dominated by larval stages (copepodid and chalimus; Table 3).

Model selection and multimodel inference suggested that exposure plus salinity was the best predictor of louse prevalence on juvenile salmon, given the set of candidate models (Table 4). Specifically, louse prevalence increased at sites of high exposure to salmon farms, and this was most prominent in the regions with the highest salmon production (Fig. 3); three of three models in the top model set (0–4 ΔAIC) contained exposure. Summing the Akaike weights ($\Sigma\omega_i$ = 0.974) across the top models ranked the variable exposure higher than salinity and temperature by factors of 2.5 and 3.8, respectively (Table 5). Although mixed-effects modelling results were broadly similar for each louse and host species, an exception was an increase in the effect of chum salmon host length on the prevalence of *C. clemensi*.

Discussion

Our study shows associations between salmon farms and infestations of sea lice on wild juvenile salmon across a large area of coastal British Columbia. Specifically, we show regional differences in parasitism of juvenile salmon between areas with and without salmon farms, as well as within-regional differences between sites of differing exposure levels. Within salmon farmed regions, juveniles at low-exposure sites hosted fewer sea lice and were most similar in infection levels to regions without salmon farms. Overall, exposure to farms was the most important factor explaining louse prevalence. Finally, the proportion of *L. salmonis* infection increases in concert with farm salmon production.

Because louse parasitism of juvenile salmon at low-exposure sites in active farm regions is most similar to levels in a region that lacks salmon farms, this suggests a "baseline" designation that can enable regional comparisons. Juvenile chum and pink salmon examined at sites of low exposure in Finlayson and the Broughton Archipelago hosted spatially uniform louse prevalence averaging less than 5%. These rates are most similar to that at Bella Bella, where farms are absent (3.5%), and correspond with those

Table 5. Summed Akaike's information criterion (AIC) weights ($\Sigma\omega_i$) across the top model set to rank parameters by relative importance in predicting sea louse prevalence on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*).

Parameter	$\Sigma\omega_i$	Direction of highest louse prevalence
Exposure	0.974	High exposure to salmon farms
Salinity	0.394	Higher salinity
Temperature	0.259	Higher temperature

Note: Exposure is fish exposure to farm influence (low or high), salinity is sea surface salinity, and temperature is sea surface temperature.

reported elsewhere in coastal British Columbia without farms (Morton et al. 2004; Krkošek et al. 2007*b*; Gottesfeld et al. 2009). However, juveniles at low-exposure sites in Georgia Strait hosted higher louse levels than those in all other peripheral areas, though levels were significantly lower than those in high-exposure locations within the region. The large number of farms in this area, the high complexity of waterways, and evidence of long-distance transmission capability of farm-origin lice (>30 km; Krkošek et al. 2006; Costello 2009) suggest that louse transmission in this region confounds point sources as previously described (Morton et al. 2008).

The consistent relationship between elevated louse levels near salmon farms over all regions examined strongly suggests farm-induced parasite transmission to wild fish. Farm fish hosting even small numbers of lice can collectively produce large numbers of louse eggs and infectious larvae (Heuch and Mo 2001; Heuch et al. 2005; Orr 2007). Both juvenile chum and pink salmon hosted elevated levels of lice in all regions and years at sites of high exposure compared with lice levels at sites of low exposure. These results are consistent with previous research in farm areas of Europe (Tully et al. 1999; Bjorn and Finstad 2002) and locally in the Broughton Archipelago and Georgia Strait (Krkošek et al. 2005*a*, 2006; Morton et al. 2008). We add to this evidence a 7.1-fold increase in louse abundance near farms in the northern region of Finlayson compared with that of sites of low exposure. Although this is the first demonstration of elevated lice levels on British Columbia's north-central coast, the lower parasitism compared to that of other farm areas is most likely due to low salmon production in the region.

Although environmental parameters have been considered as contributors to elevated louse parasitism of juvenile salmon, the data we present here suggest they are not the primary factors predicting prevalence levels in areas that are exposed to open net-pen salmon farms. Other work has shown that sea louse growth is strongly dependent on, and positively correlated with, salinity and temperature (Pike and Wadsworth 1999; Costello 2006). However, we found only moderate positive associations between salinity and louse prevalence, and only at sites of high exposure to salmon farms. Size (length) of juveniles also did little to predict louse prevalence. Instead, our analyses show that exposure to farms was the most important factor explaining louse prevalence. Moreover, louse abundance is coupled with the amount of salmon produced in a given farm region. For example, regional louse abundance (combined low- and high-exposure sites) increased from 0.13 at Finlayson, to

0.24 in the Broughton Archipelago, to 0.65 in Georgia Strait, with associated farmed salmon production of 1911, 16 174, and 17 005 metric tonnes, respectively.

A comparison of infections by the two louse species provides further insights into the potential for salmon farms to alter natural parasite dynamics. Juvenile salmon at sites of low exposure in all regions were most infected by *C. clemensi*, which is consistent with observations in other British Columbia areas where farms are absent (Morton et al. 2004; Krkošek et al. 2007*b*; Gottesfeld et al. 2009). This species is not salmon specific, unlike *L. salmonis*. However, parasitism by *L. salmonis* increased in all regions at sites of high-farm exposure and became the dominant louse infecting juveniles near Broughton and Georgia Strait farms, where farmed salmon production is highest. This proportional shift may contribute to the relationship between increased fish aquaculture intensity and decreasing wild salmon populations observed in Europe and eastern and western Canada by Ford and Myers (2008). *Lepeophtheirus salmonis* are locally associated with juvenile chum and pink salmon mortality (Morton and Routledge 2005; Krkošek et al. 2006) and have been implicated in contributing to the population collapse of pink salmon in the Broughton Archipelago (Pacific Fisheries Resource Conservation Council 2002; Krkošek et al. 2007*a*). Accordingly, these data should alert managers to the potential for high mortality of juvenile salmonids and associated population level impacts on numerous wild salmon stocks migrating through the high-intensity farm salmon production region of Georgia Strait.

Conservation implications

Sea lice from salmon farms threaten vulnerable wild salmon populations in British Columbia, heightening the urgency required for Canada to develop an effective conservation-based salmon aquaculture policy. Infection levels are correlated with the amount of salmon produced in a given farm region; the alternative explanations beyond farm-origin lice that we tested here have less support. These findings should concern resource managers, as current wild salmon populations on the coast of British Columbia are under multiple human stressors, and many populations are at low levels (English et al. 2006; Price et al. 2008). Moreover, salmon farms have been specifically implicated in the decline or collapse of several local wild salmon populations (Krkošek et al. 2007*a*; Ford and Myers 2008). Given the increased production and site expansion proposed by the salmon farm industry, associated effects from farms may intensify and ultimately challenge the sustainability of ecosystems and economies along British Columbia's entire coast (Krkošek 2010). Threats from salmon farms to wild salmon can be mitigated by reducing the number of fish per farm, limiting the number of farms in a region, and moving farms from migration routes and juvenile salmon habitats, as has been implemented in some wild salmon sensitive areas of Norway (Heuch et al. 2005; Krkošek 2010). Ultimately, a switch to land-based aquaculture offers the best solution to the problem of transmission of diseases to wild fish.

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Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*

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Abstract: As with other species, frequency-dependent selection during reproduction has long been proposed as an important mechanism in maintaining alternative male reproductive phenotypes in Pacific salmon (*Oncorhynchus* spp.). Jack salmon mature one year earlier than the youngest females in a population and are much smaller than older "adult" males. We tested the hypothesis that mating success of both phenotypes is consistent with the frequency-dependent selection model. By holding male density constant and varying the frequency of adults and jacks in eight separate breeding groups, we found that adult male access to females, participation in spawning events, and adult-to-fry reproductive success increased with their decreasing frequency in a breeding group. Jacks exhibited the same pattern (increasing success with decreasing frequency), although the relationships were not as strong as for adults. Overall, jack and adult males mated with a similar number of females, but jacks sired only 20% of all offspring. Observational data suggested that adult males benefited from sperm precedence associated with their ability to court females and enter the nest first at the time of spawning. Our work provides the first experimental evidence of frequency-dependent selection during mating in the family Salmonidae.

Résumé : Comme on l'a fait chez d'autres espèces, on a longtemps proposé la sélection en fonction de la fréquence durant la reproduction comme mécanisme important pour le maintien des phénotypes reproducteurs mâles de rechange chez les saumons du Pacifique (*Oncorhynchus* spp.). Les madeleineaux mâles atteignent la maturité une année avant les femelles les plus jeunes dans la population et sont beaucoup plus petits que les mâles « adultes » plus âgés. Nous vérifions l'hypothèse qui veut que le succès de la reproduction pour les deux phénotypes soit compatible avec le modèle de sélection en fonction de la fréquence. En maintenant constante la densité des mâles et en faisant varier la fréquence des mâles madeleineaux et adultes dans huit groupes reproducteurs différents, nous observons que l'accès des adultes mâles aux femelles, leur participation aux épisodes de reproduction et leur succès reproductif de l'adulte à l'alevin augmentent en fonction de leur fréquence décroissante dans un groupe reproducteur. Les madeleinaux mâles suivent le même patron (augmentation du succès avec une fréquence décroissante), bien que la relation ne soit pas aussi forte qu'avec les adultes. Globalement, les madeleinaux et les mâles adultes s'accouplent avec un nombre similaire de femelles, mais les madeleinaux n'engendrent que 20 % de l'ensemble des rejetons. Des observations laissent croire que les mâles adultes jouissent d'une préséance spermatique associée à leur habileté à être les premiers à courtiser les femelles et à pénétrer sur les nids au moment de la fraie. Notre travail fournit les premières preuves expérimentales de la sélection en fonction de la fréquence durant la fraie dans la famille des Salmonidae.

[Traduit par la Rédaction]

Introduction

Pacific salmon (*Oncorhynchus* spp.) males exhibit alternative reproductive phenotypes. In several species (sockeye: *Oncorhynchus nerka*; coho: *Oncorhynchus kisutch*; and Chinook: *Oncorhynchus tshawytscha*), males that mature one year earlier (termed jacks) than the youngest females in a population are substantially smaller and less sexually dimorphic than older males (hereafter adults). Theoretical models of the evolution and maintenance of alternative life history

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phenotypes in anadromous salmonids include frequency-dependent selection (FDS) during reproduction and polygenic trait thresholds that influence age-at-maturity (Hutchings and Myers 1994; Fleming 1996; Tomkins and Hazel 2007). Evidence for strong heritability in age-at-maturity in Pacific salmon comes from quantitative genetic studies (Hankin et al. 1993; Heath et al. 1994, 2002) and measures at the population level (Hard et al. 1985; Appleby et al. 2003). Physiological traits mediated by environmental conditions have been shown to trigger early male maturation (Vøllestad et al. 2004; Shearer et al. 2006), and growth thresholds for early male maturity can differ among populations of Atlantic salmon (*Salmo salar*, Piché et al. 2008).

Trade-offs between sexual selection and other forms of natural selection may also shape the frequency of alternative phenotypes in a population. Jacks benefit from higher survival to maturity owing to their reduced time spent at sea or from reduced predation or other forms of ecological selection during reproduction (Quinn et al. 2001). Nevertheless, jacks often represent a small portion of breeding populations of sockeye, coho, and Chinook salmon (Myers et al. 1998; Appleby et al. 2003; Carlson et al. 2004). This may partly reflect disadvantages of small size and reduced access to females during reproduction (Carlson et al. 2004). Surprisingly, the natural relative mating success of jack and adult male Pacific salmon has received very little attention. Van Doornik et al. (2002) estimated the effective proportion of coho salmon jacks in two naturally spawning populations to be 35%, compared with only 2% in a hatchery population. Gross (1985) indirectly estimated mating success in coho salmon jacks at 66% that of older males. The only direct evaluation of jack mating success in Pacific salmon comes from Foote et al. (1997), who used genetic markers and quantified the relative success of seven sockeye salmon jacks in 3.5 m by 3.5 m cages and found highly variable breeding success (3% to 97%; average = 42%) relative to that of older males.

Pacific salmon adult males fight for primary access to females and thus the ability to engage in courtship and spawn with them. Losers often establish "satellite" positions downstream of the courting pair, from which they attempt to "sneak" spawn, and may be excluded from breeding opportunities altogether. The smaller jacks very rarely challenge larger males for courtship opportunities and instead compete for lower positions in hierarchies or hide and wait for opportunities to sneak spawn. Just as adults are not obligate consorts, jacks are not obligate sneakers. Jack Chinook salmon will court and spawn with females in the absence of larger males, and when doing so exhibit high fertilization success (Berejikian et al. 2000; Berejikian and Tezak 2005).

Some fishes display genetically based reproductive polymorphisms that are maintained by FDS (Dijkstra et al. 2008; Hurtado-Gonzales and Uy 2009). FDS favors the rare form, wherein the fitness of one form decreases as it becomes relatively more frequent in the population. Male intrasexual competition, which is very intense in Pacific salmon, has recently been proposed as an important mechanism causing frequency dependence in other taxa (van Doorn et al. 2004). Gross (1985) predicted that increases in the number of jack coho salmon would reduce their proximity to the female and decrease their fitness. Hutchings and Myers (1988) tested the relationship between sneaker male (mature male parr Atlantic salmon) frequency and mating success, but did not control for male density and therefore could not distinguish between the effects of density and frequency dependence (see Bleay et al. 2007).

In the present study, we quantified jack and adult male Chinook salmon breeding behavior, their proximity to females prior to and during spawning, and conducted DNA-based pedigree analyses to obtain measures of their adult-to-fry reproductive success. We tested for FDS by varying the ratio of jack and adult males in eight separate breeding groups to quantify the effects of jack and adult male frequencies on access to breeding opportunities, participation in observed spawning events, and individual reproductive success. Male density was held constant to avoid confounding frequency dependence with density dependence, and as such this represents the first experimental test of FDS on alternative life history strategies in a salmonid.

Materials and methods

Adult spring Chinook salmon were obtained from the Trask River Hatchery, located on the Trask River, Oregon. Twelve females and 32 males were collected and transported on each of two dates (5 and 12 September 2007) in an oxygenated transport tank to the Oregon Hatchery Research Center, located on Fall Creek approximately 3 h from the Trask River Hatchery. Upon arrival, the fish were held overnight in 4 m diameter tanks supplied with Fall Creek water. The following day, each adult Chinook salmon was anesthetized (MS-222: tricaine methanesulfonate), weighed (nearest g), measured for fork length and postorbital–hypural (POH) length (nearest mm), and externally tagged with a uniquely numbered Petersen disc tag. A portion of the anal fin was removed and preserved in 100% nondenatured alcohol for genetic analysis. This procedure was repeated the next year (3 and 10 September 2008).

Six female and 16 male Chinook salmon were stocked into each of two replicate spawning channels on 6 and 13 September 2007 and two additional channels on 4 and 11 September 2008. The nearly 3:1 male to female sex ratio was established to mimic natural operational sex ratios (ratio of sexually active males to sexually active females). Even when sex ratios are nearly equal, the operational sex ratio can be much greater than one because of the longer breeding duration of males (cf. Hamon et al. 1999). We intentionally varied the number of jack and adult males among the four channels within each year (Table 1). Females from Oregon coast Chinook salmon populations mature at age-3 or older; therefore jacks mature at age-2 (Hankin et al. 1993). The body sizes of jacks (age-2) and adult males (age-3 and age-4) stocked into each section are also shown (Table 1). At the time of stocking, we considered males less than 430 mm POH to be jacks based on Hankin et al. (1993). All fish of this size were morphologically characteristic of jacks (no pronounced secondary sexual characteristics), and subsequent scale analyses indicated that agreement between scale age and size-based determination of male phenotype was 98.4% (126 out of 128 total males).

Each meandering spawning channel measured 8 m wide by 65 m long and contained a mixture of substrates ranging

Table 1. Stocking date, jack frequency, and average (standard deviation in parenetheses) postorbital–hypural (POH) length (mm) of Chinook salmon males stocked into each of the four stream channels in 2007 and 2008.

			POH			
Channel	Stocking date	Jack frequency	Adult	Jack	Spawnings observed	Fry collected (sampled)
2007						
A	12 Sept.	8	604 (42)	369 (19)	9	3010 (301)
B	12 Sept.	4	603 (40)	388 (11)	12	5972 (641)
C	5 Sept.	6	541 (61)	394 (24)	2	5198 (572)
D	5 Sept.	5	607 (42)	397 (21)	3	3682 (363)
2008						
A	10 Sept.	6	583 (20)	400 (18)	6	—
B	10 Sept.	4	554 (39)	391 (29)	10	—
C	3 Sept.	10	604 (42)	401 (20)	11	—
D	3 Sept.	8	561 (36)	400 (19)	14	—

Note: The number of adult males in each section equaled 16 minus the number of jacks. Six females were stocked into each section. The total number of spawning events observed and the number of fry collected from each channel (number sampled for DNA pedigree analyses in parentheses) are also shown.

from coarse sand to large cobbles. Each channel contained several meanders, pool–riffle sequences, and large woody debris, placed in such manner that each channel was a very close replicate of the others. Shade cloth was suspended above the streams. Water was diverted from Fall Creek, through a settling pond and then to each channel to provide approximately 0.043 $m^3 \cdot s^{-1}$ per channel. Airlift pumps were used to partially recirculate water through the channels to create a total flow of approximately 0.06 $m^3 \cdot s^{-1}$ in each channel.

Behavioral observations were conducted from dawn to dusk in each channel from the time the fish were introduced until the last female in each channel was no longer sexually active (i.e., no longer nest building). We scanned each of the stream channels multiple times each day to document the activity of each female, and we conducted focal sampling of females that were constructing nests and preparing to spawn. When a female was determined to be constructing a nest, we characterized the male dominance hierarchy surrounding the female. The "dominant" male had primary access to the female, exhibited courtship behaviors (crossing over and quivering), and chased off other males positioned either downstream or upstream of the female. "Satellite" males held positions typically downstream of the courting pair, were frequently chased by the dominant male, and would occasionally sneak into the nest pocket prior to and during spawning. The satellite maintaining closest proximity to the female was designated "S1", the second closest was "S2", and so on. We included males that hid or adopted what have been referred to as "sneaker" tactics (Gross 1985; Healey and Prince 1998) as satellites, because males would often switch between fighting and sneaking behaviors within the same hierarchy. Dominant and satellite males were determined to have participated in a "hierarchy", and the number of hierarchy participations was tabulated for each male over the course of the spawning season.

We attempted to observe as many actual spawning events as possible and record the males that participated in each event and their order of nest entry at the time of spawning. Only instances in which females crouched in the nest pocket, gaped, were accompanied by at least one gaping male, and covered their eggs with a rapidly increased rate of digging (Berejikian et al. 2000) were considered actual spawning events. These were discriminated from false spawning events in which females do not engage in egg covering. We tabulated the frequency of spawning participations for each male and categorized them by rank order of nest entry (1 = first to enter, 2 = second to enter, etc.).

In 2007, channels C and D were stocked and monitored first. The pace of spawning was quicker than we had anticipated, and we did not continuously observe nesting females for long enough periods of time and as a result we missed observing some spawning events. However, in channels A and B (i.e., the second group of fish stocked in 2007), and in all four channels in 2008, we are certain we observed all spawning events that occurred between dawn and dusk because no nesting females were subsequently observed cover digging or constructing new nests (see Berejikian et al. 2007 for details on digging frequencies in Chinook salmon) without our having observed a spawning. Much spawning occurred at night in both channels that was not observed. Thus, the behavioral data reflect only daytime activity, and the reproductive success estimates reflect breeding that occurred throughout the study (day and night).

To quantify individual reproductive success of Chinook salmon spawning in 2007, emergent fry were removed from the stream channels by seining and electroshocking on 29 and 30 January 2008. All channels were sampled again on 25 February 2008, and the channels were dewatered to ensure that all fry were collected. We counted the total number of fry from each channel and subsampled at a similar rate among channels (Table 1). Subsampled fry received a lethal dose of MS-222, and their caudal fins were preserved in 100% nondenatured alcohol for DNA pedigree analyses. Fry offspring were not collected from Chinook salmon spawning in 2008 because eggs from individual nests were intentionally excavated when the eggs were at the eyed stage of development as part of a related study to estimate fertilization success of males at different positions in the hierarchy. Thus, we have adult-to-fry reproductive success estimates for four separate breeding groups at four jack–adult ratios from the 2007 spawning season, but not from 2008 (Table 1). Hereafter, we refer to the different jack–adult ratios shown (Table 1) as "jack frequencies" and present the number of jacks within each breeding group (the number of adults is always 16 minus the number of jacks).

Genomic DNA was extracted from the adult and offspring tissue samples and subjected to polymerase chain reactions (PCR) to amplify eight microsatellite loci: Ogo4 (Olsen et al. 1998); Oki100 (K.M. Miller, Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada, unpublished data); Omm1080 (Rexroad et al. 2001); Ots3M (Greig and Banks 1999); Ots9 (Banks et al. 1999); and Ots211, Ots212, and Ots213 (Greig et al. 2003). A fragment analysis was conducted on the PCR products using an Applied Biosystems 3100 genetic analyzer, and Genescan and Genotyper software (Applied Biosystems) was used to determine the genotypes of every individual for each locus. Offspring that were unable to be genotyped for four or more loci were dropped from further analyses. The genotypes of the offspring were then compared with those of the adults using the computer program CERVUS 3.0 (Kalinowski et al. 2007) to determine the parentage of each fry. Parentage assignments had to meet the 95% confidence level to be included in further analyses.

The number of focal sampling observations made on male hierarchies surrounding 46 of the 48 nesting females stocked into the spawning channels in 2007 and 2008 (two females died prior to spawning) ranged from 58 to 198 (N = 878). Therefore, within each breeding group, we calculated the proportion of observations in which each male was observed in the dominant and satellite positions in prespawning male hierarchies. We also calculated the proportion of actual spawning observations in which each male spawned as the first, second, third, fourth, or fifth to enter the nest and the total number of spawning participations. The prespawning hierarchy proportions and actual spawning proportions were angular (arcsine square-root) transformed to improve normality. The ability of individuals to achieve each status within a prespawning hierarchy and to participate in spawning events was analyzed by two factor analyses of variance (ANOVAs) with male phenotype (jack or adult) and jack frequency as the main effects. Separate ANOVAs were conducted for each year. We calculated the average rank order of nest entry at spawning for each phenotype within a breeding group. Similar patterns were evident among breeding groups (see Results), so we used a t test on the combined data to compare the rank order of nest entry between jack and adult males. In 2007, individual reproductive success was calculated as the number of fry per male spawner and expressed as a proportion of the total number of fry produced in its respective channel. Angular transformed proportions were analyzed by the same ANOVA model as the behavioral measures. A regression analysis was performed to test for a linear relationship between the average reproductive success of each phenotype within a breeding group and its frequency.

Results

Adult males competed primarily among themselves to establish dominance and attain courtships with nesting females. Adult males also competed among themselves and with jacks for satellite positions in the hierarchies. Adult males attained the dominant position in prespawning male hierarchies more frequently than jacks in both 2007 and 2008 (Table 2). Adult males were observed significantly more often than jacks in the first satellite (S1) position in 2008, but not in 2007 (Table 2). Jacks were significantly more often observed in the S2 position in 2007 and S3 position in 2008 (Table 2). There were no significant interactions between jack frequency and male phenotype on participation at any level within the prespawning hierarchies (Table 2).

Jacks used a number of different tactics to maintain positions in hierarchies and position themselves for spawning. Jacks often mimicked female coloration patterns (dark lateral stripe), hid under logs or in side channel pools, held positions in very shallow water downstream from nests where larger males appeared reluctant to chase them, and held positions alongside or downstream of larger males. From these peripheral positions, they periodically darted into the nest to position themselves for spawning. Jacks did court females, but it was very infrequent and typically occurred shortly after females had spawned or were still hours away from their next spawning event when adult males less vigorously defended females.

We observed a total of 67 spawning events (Table 1), 27 (40%) of which involved a single male participant, while the remainder included from two to five participants. Participation in prespawning hierarchies was a significant predictor of participation in observed spawning events ($P < 0.05$ for all linear regressions; Fig. 1). In 2007, there was a significant interaction effect between male phenotype and jack frequency on spawning participation (Table 2). Jack participation in spawning events decreased and adult male participation increased with increasing jack frequency (Fig. 2). The interaction term was not significant in 2008 (Table 2, Fig. 2). However, in the group containing four jacks in 2008, all jacks were dead by 14 September before 80% of the observed spawning events had occurred. The premature deaths were caused by injuries from one adult male that repeatedly chased, bit, and shook all of the jacks. We did not observe comparably violent aggression or premature jack deaths to this extent in the other seven breeding groups. Although the statistical analyses of spawning success in 2008 include the breeding group with four jacks, it is important to recognize that the greater spawning success of adult males in this group reflects the absence of jacks and a different mechanism affecting reproductive success than in the other seven breeding groups.

Adult males participated in a significantly greater number of spawning events than jacks in 2008, but not in 2007 (Table 2). Adult males were significantly more often observed as the first to enter the nest during spawning than jacks in both years (Table 2). In fact, jacks were observed as the first male to enter the nest on only two occasions. There were no significant differences between jack and adult males in their spawning frequency as the second or third

Table 2. Tests for effects of male phenotype and jack frequency by male phenotype interactions on behavioral measures of breeding success.

	Phenotype			Phenotype × frequency	
	F	*P*	Greater	*F*	*P*
2007					
Spawning participations	0.013	0.910	NS	7.03	**0.013**
First to enter	4.78	**0.037**	**Adult**	0.85	0.364
Second to enter	1.13	0.297	NS	11.10	**0.002**
Third to enter	2.57	0.120	NS	0.46	0.502
Total courtships	10.48	**0.002**	**Adult**	0.43	0.729
Dominant	13.89	**<0.001**	**Adult**	0.28	0.841
S1	0.85	0.359	NS	0.68	0.571
S2	5.74	**0.020**	**Jack**	1.77	0.164
S3	2.27	0.137	NS	1.45	0.237
2008					
Spawning participations	9.84	**0.003**	**Adult**	1.99	0.126
First to enter	9.13	**0.004**	**Adult**	0.64	0.591
Second to enter	2.37	0.130	NS	0.52	0.669
Third to enter	0.03	0.873	NS	3.64	**0.018**
Total courtships	35.85	**<0.001**	**Adult**	0.20	0.894
Dominant	35.01	**<0.001**	**Adult**	0.47	0.707
S1	9.49	**0.003**	**Adult**	0.35	0.790
S2	17.26	0.512	NS	2.15	0.105
S3	12.23	**0.001**	**Jack**	0.98	0.409

Note: *F* tests and *P* values from the analyses of variance (ANOVAs) for the main effect of male phenotype (jack or adult male) and the interaction between jack frequency and male phenotype are shown. The phenotype with the greater mean value is shown where there were significant effects ($P < 0.05$, in bold; NS = nonsignificant). The total spawning participations and order of nest entry in 2007 include analysis of breeding groups that contained four or eight jacks. The groups that contained five or six jacks were excluded because too few spawning events were observed (see Table 1). S1, closest satellite position; S2, second closest position; S3, third closest position.

Fig. 1. Frequency of participation in observed spawning events plotted against frequency of participation in prespawning hierarchies. Each point represents a different male and each symbol represents a different breeding group. In 2007, solid triangles = four jacks and open triangles = eight jacks. In 2008, open circles = four jacks, solid diamonds = six jacks, solid circles = eight jacks, and open diamonds = ten jacks. All six correlation coefficients were significant ($P < 0.05$). Analyses from channels C and D in 2007 were not conducted because too few spawning events were observed.

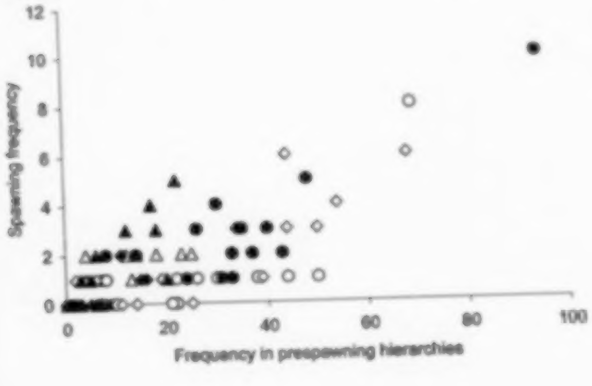
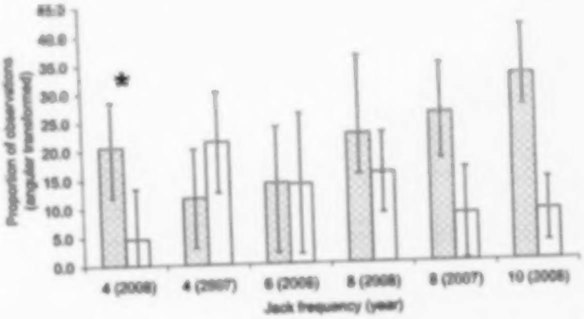
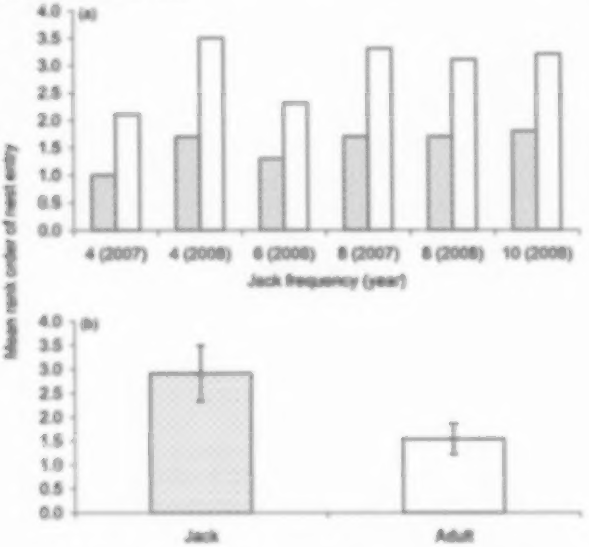


Fig. 2. The average proportion (±95% confidence interval, CI) of observed spawning events in which adults (open bars) and jacks (stippled bars) participated. The number of jacks in each of the independent breeding groups is shown on the *x* axis with the year in parentheses. The asterisk next to the 4 jack group in 2008 indicates that all jacks had died prior to 80% of the observed spawning events, so all subsequent participations were limited to adult males.



male to enter the nest during spawning in either year (Table 2). There were significant phenotype by jack frequency interactions for the participation as the second male to enter the nest in 2007 and third to enter in 2008 (Table 2). In both cases, jack and adult male success in spawning from a satellite position was inversely related to their frequency

Fig. 3. (*a*) Average rank order of nest entry for jack (stippled bars) and adult (open bars) males. Lower ranks entered the nest sooner than higher ranks (i.e., the first male to enter the nest at the time of spawning was given a rank of 1, second to enter had a rank of 2, and so on). Panel (*b*) shows averages and 95% confidence intervals for the combined data.

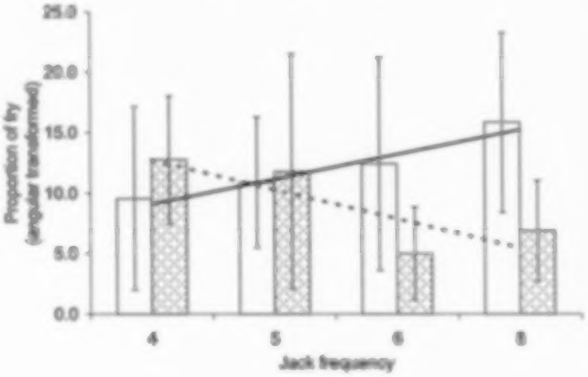


in a breeding group. Overall, adult males had a significantly lower rank order of nest entry (i.e., entered the nest earlier, $t = 11.316$, $P < 0.01$), and the difference was fairly consistent across the range of jack frequencies (Fig. 3).

We assigned parentage to 1877 offspring from the four breeding groups in 2007. Nine offspring were dropped from the analyses because they could not be genotyped for at least four loci. All parentage assignments met the 95% confidence level. All of the females, except for the two that died prior to spawning, produced offspring in the 10% subsamples of the four fry populations, so the male reproductive success results reflect matings that occurred in two breeding groups with five females each (n = 5 jacks and n = 6 jacks) and two breeding groups with six females (n = 4 jacks and n = 8 jacks).

The interaction between phenotype and jack frequency on adult-to-fry reproductive success was nonsignificant ($F_{[3,56]}$, $P = 0.345$; Fig. 4). The regression analysis did indicate that average adult male reproductive success increased significantly with increasing jack frequency (and decreasing adult frequency, $n = 4$ breeding groups, $r^2 = 0.93$, $P = 0.031$; Fig. 4). The average jack reproductive success declined with increasing jack frequency, but the correlation was not significant ($n = 4$, $r^2 = 0.56$, $P = 0.23$; Fig. 4). The relationships between frequency and reproductive success had a stabilizing effect on the total proportion of fry sired by the two male phenotypes in each breeding group. In the breeding group with the fewest jacks, 21% of all fry (i.e., fry per jack × the number of jacks) were sired by jacks, which was very close to their proportion in the breeding group (25%). Jacks collectively sired 33%, 9%, and 19% of the fry frequencies of five, six, and eight jacks per breeding group, respectively. The combined average jack contribution across all four breeding groups in 2007 was 20.3% and did not differ significantly from the total adult contribution (79.7%, $F_{[1,56]} = 1.23$, $P = 0.27$). Jack and adult males mated with a similar number of females across all breeding groups (2.0 mates per adult male and 2.1 mates per jack), but the number of offspring produced per mating was significantly less for jacks (10.2 per mate) than for adult males (23.6 per mate, $t = 2.64$, $P = 0.011$).

Fig. 4. Average (±95% confidence interval, CI) proportion (angular transformed) of offspring produced within each breeding group for jack (stippled bars) and adult males (open bars). The lines reflect least squares regression analysis testing for linear relationships between jack frequency and mean reproductive success values ($N = 4$ breeding groups) for jack (dashed line, $r^2 = 0.56$, $P = 0.26$) and adult males (solid line, $r^2 = 0.93$, $P = 0.03$).



Discussion

As expected, adult males competed for courting opportunities, in many cases monopolizing access to females, and spawned as the lone male participant in over one-third of the observed spawning events. The finding that the much larger adult males dominated access to females is not surprising given the large body of literature indicating that larger salmonid males tend to have a breeding advantage over smaller males (reviewed by Esteve 2005). Jacks participated almost exclusively by sneaking into the nest from satellite positions and sired 20.3% of all progeny that were genotyped.

Sperm quality, ejaculate volume, and precedence (timing of contact with the egg) could all potentially affect fertilization success. It is unclear from this study whether the later timing of nest entry of jacks participating in multiple-male spawning events impaired their fertilization success, because we could not differentiate between offspring that were produced from single pair matings and those produced during multiple-male spawning events. In rainbow trout, sperm volume did not affect fertilization rate and males did not adjust milt volume based on male competitor presence (Fitzpatrick and Liley 2008). In Chinook salmon, jack and adult males were equally capable of fertilizing eggs during natural spawning when each phenotype was paired as the lone consort with an individual female (Berejikian and Tezak 2005).

In the present study, the finding that jacks entered the nest later and had lower reproductive success and significantly fewer offspring per mate is consistent with the hypothesis that sperm precedence influenced fertilization success in multiple-male spawning events. Sperm precedence effects have been inferred in other studies on chum salmon (*Oncorhynchus keta*: Schroder 1981), sockeye salmon (Chebanov et al. 1983), and iteroparous Atlantic salmon (Mjølnerød et al. 1998) and brook trout (*Salvelinus fontinalis*: Blanchfield et al. 2003).

The significant positive correlation between jack frequency and average adult male reproductive success, the significant interactions between male phenotype and jack frequency for total spawning participations in 2007, and the sneak spawning opportunities (second and third to enter the nest during spawning) indicate support for the FDS model. Although a significant interaction for total spawning participations was not detected in the 2008 data, the patterns were similar to those in 2007 except for the breeding group containing the fewest number of jacks (four) for the reasons mentioned in the Results. The present study is the first to our knowledge to experimentally test the hypothesis of FDS in salmonids. Gross (1985) found that intermediate-sized coho salmon males maintained distances further from nesting females than did larger adult males and smaller jacks, suggesting disruptive selection on male size. In Atlantic salmon, the average proportion of eggs fertilized by mature male parr, which are an order of magnitude smaller than anadromous males, decreased with their increasing frequency in the population (Hutchings and Myers 1988). However, parr frequency increased with total male density, so density dependence could not be separated from frequency dependence. Evidence for FDS, controlling for density dependence, has been clearly demonstrated in lizards (Sinervo and Lively 1996; Bleay et al. 2007), where it functions to maintain genetic color polymorphisms that have a high heritability (96%).

Is frequency-dependent mating in salmon a result of intrasexual male competition or female choice? Male phenotypic diversity in other fishes may evolve and persist through male competition (Dijkstra et al. 2008) or as a mechanism to circumvent female choice (Hurtado-Gonzales and Uy 2009). Evidence for female choice comes from females delaying nest construction in the presence of smaller (putatively less preferred) males (Foote 1989; Berejikian et al. 2000; but see Allen et al. 2007). However, male competition for access to females is very intense, appears to constrain female choice, and strongly influences mating patterns in salmonids. We hypothesize that the evidence for FDS in the present study resulted from male competition within life history phenotypes. That is, when jacks were abundant they competed for fewer satellite and sneak spawning opportunities per individual jack, and when adult males were abundant there were fewer courting opportunities per individual. Furthermore, we observed some evidence of jacks mimicking female coloration patterns. Female Chinook produce a thick lateral band as spawning nears, which becomes continuous just prior to spawning, then dissipates and reappears just prior to each subsequent spawning event. Jacks in our study, and some satellite adult males, mimicked female spawning coloration by producing and maintaining a dark, thick band along the lateral line, which we suspect functions to reduce competitive pressure (attacks) from the dominant male.

In Atlantic salmon, alternative male life history phenotypes are presumed to be maintained by FDS, for which there is some support (Hutchings and Myers 1988). Atlantic salmon age-at-maturity is best modeled as a threshold trait rather than purely status-dependent, because it is heritable and differs among populations and among individuals within a population (Piché et al. 2008). Growth rate and attainment of a threshold body size determines whether an individual will mature. Evidence for strong heritability for age-at-maturity (Heath et al. 2002), similar growth and body size triggers for early male maturation (Larsen et al. 2004; Shearer et al. 2006), and the evidence of FDS provided in the present study suggest that alternative male phenotypes in Chinook salmon may be most accurately modeled in a manner similar to that for Atlantic salmon.

To the extent that age-at-maturity of Chinook salmon populations fits the threshold trait model, it may be strongly influenced by anthropogenic forces. Most notably, the majority of Chinook salmon along the west coast of the USA and Canada are now produced from hatcheries (Naish et al. 2008). During the artificial spawning process, hatchery operators may exert intentional and unintentional bias regarding the inclusion of jack gametes that may reduce jack contributions in coho salmon (Van Doornik et al. 2002). Even random mating schemes in hatchery programs may significantly alter age-at-maturity of the offspring in Chinook salmon (Hankin et al. 2009). Currently, Pacific salmon hatchery operations in the USA follow no explicit scientifically based guidance regarding the appropriate level of jack inclusion during artificial spawning. However, Hankin et al. (2009) have proposed a model where matings would be restricted pairings in which male length exceeds female length to avoid reducing age-at-maturity. Data from the present study might suggest that hatchery broodstock management should be sensitive to changes in the relative abundance of jack and adult males where mimicking natural life history patterns and selection processes is a management objective. Generally, our data suggest that a greater per capita contribution should come from adult males when they are relatively rare in the population, and a lower per capita contribution from a greater number of individuals may be more appropriate in years when the adult to jack ratio is high. In many river systems, weirs are deployed to count, sample, and in some cases control the abundance of hatchery and natural spawners. Our data suggest that jacks not be excluded intentionally because contribution will be stabilized to some degree by FDS. However, other anthropogenic forces such as size-selective harvest (Hankin and Healey 1986; Hankin et al. 2009) and hatchery rearing methods that promote high juvenile growth rates and early male maturation (e.g., Knudsen et al. 2006) should be considered as well.

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Spawning phenology and habitat use in a Great Plains, USA, stream fish assemblage: an occupancy estimation approach

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Abstract: Knowledge of basic life-history attributes, paired with unbiased estimates of species distribution, is critical for the effective conservation of sensitive fish species. We quantified the spawning phenology, habitat use, and detectability for larvae of an assemblage of threatened Great Plains, USA, stream fishes using new occupancy estimation methods. Spawning by six Great Plains fish species occurred from April through July, and was likely initiated by changes in water temperature and photoperiod. Habitat size and type were important factors influencing the occupancy of larvae in spawning habitats. Detectability of larvae differed among species and over time, and was influenced by habitat depth and fish size. Our models indicated that multiple samples from individual habitats within a season are needed to adequately detect and predict occupancy by stream fish larvae. Conservation efforts for imperiled Great Plains fish assemblages should focus on sustaining flows that maintain a sufficient density and size of habitats needed for successful spawning and recruitment. The occupancy estimation and modeling methods employed here will be useful in developing comprehensive, unbiased programs to monitor the reproductive success of Great Plains stream fishes.

Résumé : La conservation efficace des espèces sensibles de poissons requiert une connaissance des caractéristiques fondamentales de leur cycle biologique, de même que des estimations non faussées de leur répartition. Nous avons déterminé la phénologie de la reproduction, l'utilisation de l'habitat et la détectabilité des larves dans des peuplements de poissons menacés des Grandes Plaines, É.-U., à l'aide de nouvelles méthodes d'estimation de l'occupation. La fraie de six espèces de poissons des plaines a lieu d'avril à la fin de juillet et est vraisemblablement déclenchée par la température de l'eau et la photopériode. La taille et le type de l'habitat sont des facteurs importants qui influencent l'occupation des habitats de fraie par les larves. La détection des larves varie d'une espèce à l'autre dans le temps et est influencée par la profondeur de l'habitat et la taille des poissons. Notre modélisation indique qu'il faut de multiples échantillons provenant de chaque habitat au cours d'une saison pour détecter adéquatement et prédire l'occupation du cours d'eau par les larves de poissons. Les efforts de conservation des peuplements de poissons menacés des Grandes Plaines devraient se concentrer sur le maintien de débits qui assurent une densité et une taille d'habitats suffisantes pour une fraie et un recrutement réussis. Les méthodes d'estimation de l'occupation et de modélisation que nous avons employées pourront servir à mettre sur pied des programmes complets et non faussés de surveillance du succès reproductif des poissons des eaux courantes dans les plaines.

[Traduit par la Rédaction]

Introduction

Streams on the Great Plains of North America are extremely variable environments (Matthews 1988; Dodds et al. 2004), and fishes often occupy habitats in which physicochemical conditions are near thresholds for survival. Over the past 100 years, streams on the Great Plains have been highly altered by humans (Fausch and Bestgen 1997). These alterations have exacerbated the already harsh environmental conditions and caused declines in populations of native fishes, owing to a combination of factors including the construction of impoundments (Bonner and Wilde 2000; Falke and Gido 2006), habitat fragmentation and groundwater depletion (Dudley and Platania 2007; Falke et al. 2010*a*), and habitat alteration and loss (Cross and Moss 1987). For example, in Colorado 20 of 38 fish species native to the western Great Plains are extirpated or listed as endangered, threatened, or of special concern by the state (Fausch and Bestgen 1997; CDOW 2007; Falke 2009). As a result, assemblages of Great Plains stream fish assemblages are especially in need of conservation attention.

Successful recruitment is vital for maintaining populations of the remaining Great Plains fishes, yet the environmental conditions (i.e., cues) that initiate successful spawning in these species are poorly understood. Although some Great Plains fishes may be able to spawn throughout summer, re-

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productive potential, output, and recruitment are most likely highest early in the reproductive season, owing to increasingly harsh environmental conditions as summer progresses (Bonner 2000; Durham and Wilde 2008; Falke et al. 2010*b*). Additionally, interactions among environmental factors (e.g., flow and thermal regime, photoperiod) that serve as cues may be important. Quantifying the relationship between environmental conditions and initiation of spawning is vital for understanding recruitment dynamics in Great Plains stream fishes.

Accurate, unbiased estimates of species occurrence and the relative abundance of fish larvae in spawning habitats are also important for understanding both the basic ecology of species, as well as evaluating population-vital rates and conservation status. A main source of error in many sampling and monitoring programs is caused by imperfect detection (i.e., detectability, $p < 1$), which can bias estimates of habitat occupancy and relative abundance, as well as estimates of the effects of predictor variables (Tyre et al. 2003; Gu and Swihart 2004). Recently, statistically rigorous methods have been developed to estimate the probability of detecting a species at occupied sites, based on multiple site visits (MacKenzie et al. 2002, 2006). These models have been extended to include multiple states (e.g., absent, present at low abundance, present at high abundance), while incorporating the influence of nondetection and habitat covariates (Royle and Link 2005; Nichols et al. 2007; MacKenzie et al. 2009). This class of models is particularly appealing when species are distributed heterogeneously among habitats, there is high variance in counts among replicate samples, and the true state at a site (i.e., presence or absence) is not always observed, all of which are common when sampling the early life stages of fish (Hildén and Urho 1988; Cyr et al. 1992).

Although there have been a number of independent efforts to incorporate nondetection into occupancy estimation (Bayley and Peterson 2001; Nichols and Karanth 2002; Tyre et al. 2003), the approach developed by MacKenzie et al. (2002, 2003) is the most flexible, and has been cited in over 350 peer-reviewed publications. These models and associated variations have been applied to stream vertebrates (e.g., Kroll et al. 2008; Grant et al. 2009), but have rarely been applied to fishes (but see Burdick et al. 2008; Hayer and Irwin 2008 for applications and Wenger and Freeman 2008; Wenger et al. 2008 for model extensions). Additionally, to our knowledge, occupancy models have never been used for larval fishes.

We addressed gaps in our knowledge of the phenology and spawning habitat relationships of an assemblage of Great Plains stream fishes in the Arikaree River basin, Colorado, a harsh intermittent Great Plains stream. Specifically, our objectives were to, (*i*) evaluate the effectiveness of two common sampling methods for collecting stream fish larvae, (*ii*) develop a phenology for larval fishes in the Arikaree, and compare spawning timing with environmental factors that may act as cues, and (*iii*) use new occupancy estimation and modeling methods to investigate how habitat characteristics influence occupancy and relative abundance of larvae in spawning habitats. We also quantified habitat characteristics (e.g., depth) that may influence detectability of larval stream fishes, and use this information to suggest improved sampling methods for the future.

Materials and methods

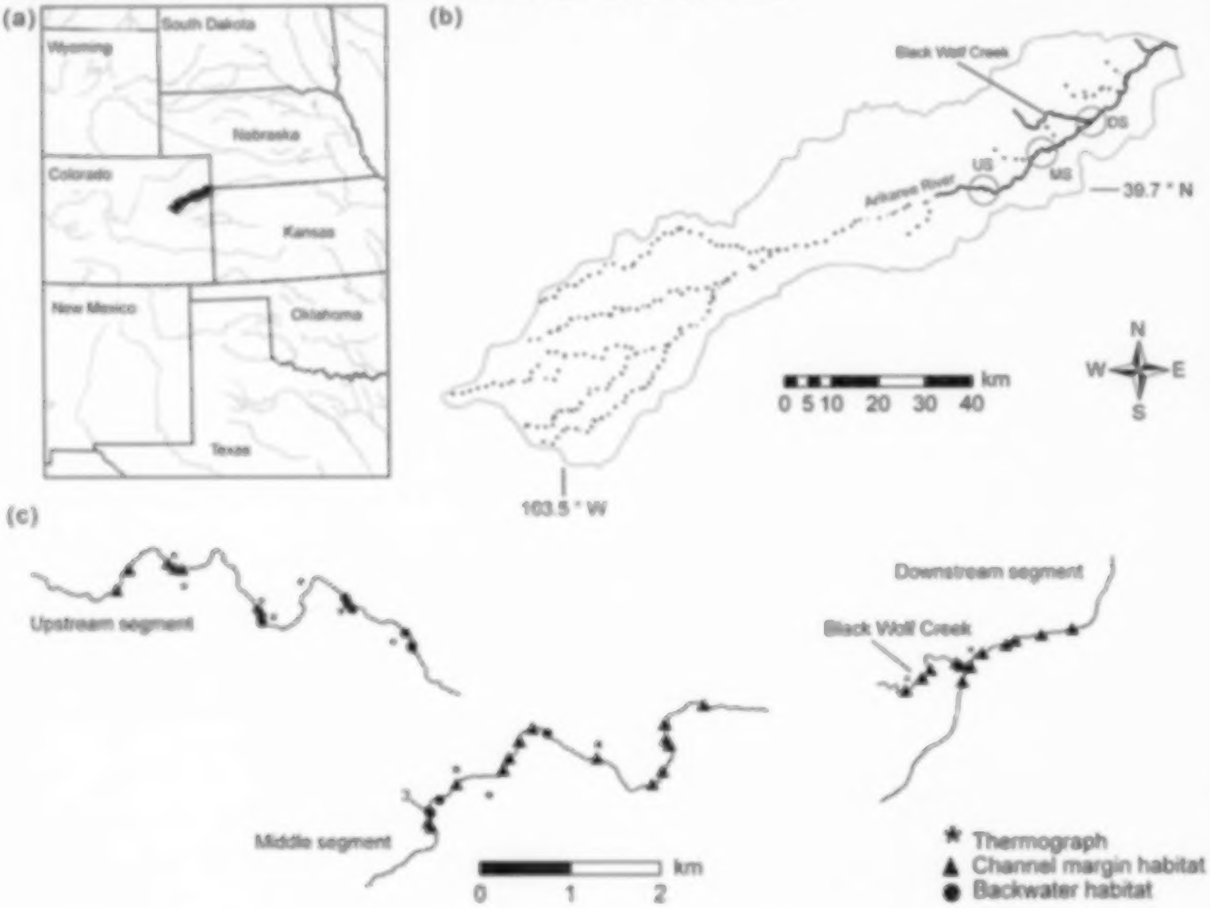
Study area and field methods

Our study area was restricted to the lower half of the Arikaree River basin, Colorado, USA, because segments with the potential for perennial streamflow and fish habitats occur only in the lower 110 km of the basin (Scheurer et al. 2003; Falke et al. 2010*a*; Fig. 1). We sampled the larval fishes and spawning habitats within three 6.4 km segments studied by Scheurer et al. (2003). These study segments were selected to represent a gradient in intermittency, from the more perennial upstream segment, to the intermittent middle segment, to the downstream segment that dries almost completely by early summer. Based on flight survey data (Falke et al. 2010*a*), these study segments encompassed approximately 20% of the total flowing habitat in the basin during late spring and early summer, the period in which we hypothesized spawning would be most likely for this fish assemblage.

The upstream segment is located within The Nature Conservancy's (TNC) Fox Ranch, and long reaches sustain flow in all but the driest periods. This segment is characterized by alternating runs and deep, persistent pools. Beaver (*Castor canadensis*) increased their activity after 2001, and created large pools in some reaches of this segment. The middle segment is made up of State Trust Lands in conservation easement administered by the Colorado Division of Wildlife (CDOW) and is largely intermittent most of the year. Its upper portion has deep, well-developed pools and an extensive gallery forest of riparian cottonwood (*Populus deltoides*), whereas its lower portion is wide and shallow with mostly sand substrate and no riparian canopy. The downstream segment flows through private lands (approximately two-thirds) and the CDOW Simmons State Wildlife Area, and is dry most of the year. A few pools persist at its upper end in some years. However, a perennial tributary, Black Wolf Creek, enters the Arikaree River in the middle of this segment and often sustains a short reach of flowing habitat in the main channel downstream of this confluence.

In the last week of March 2007, all potential spawning habitats in each of the three segments and the lower 1 km of Black Wolf Creek were identified and georeferenced using a Global Positioning System. Fishes had been captured in these habitats as spawning adults (i.e., gravid or showing spawning coloration) or larvae during previous sampling (Scheurer et al. 2003; Falke 2009; J. Falke and K. Fausch, unpublished data). Based on these data, we inferred that these habitats were used for both spawning and early rearing by this fish assemblage. Each habitat was then sampled for larvae at least every other week through the end of July. Spawning habitats were classified as backwaters or channel margins. Backwaters were relatively large, deep, off-channel habitats connected to the main channel, but with little or no flow. Channel margin habitats were relatively small, shallow, flowing areas along the main channel where higher stream flows in spring inundated terrestrial vegetation. Substrate composition within backwater and channel margin

Fig. 1. (*a*) Study area in the Arikaree River basin in northeastern Colorado, and (*b*) the location of three 6.4 km study segments (US, upstream segment; MS, middle segment; DS, downstream segment) and Black Wolf Creek. Unbroken lines in the lower basin illustrate where the potential for perennial stream flow remained in 2007 (based on Falke 2009). In (*c*) the locations of 45 spawning habitats and 12 thermographs are shown. A cluster of three backwaters in the upper middle segment is indicated.



habitats was relatively homogenous, consisting entirely of fine materials (e.g., silt and sand; Falke 2009).

During the first week of sampling, we measured three main attributes of spawning habitats that we predicted would most influence occupancy, abundance, and detectability of larval fishes. These included surface area, maximum depth, and water temperature. The surface area of each habitat was quantified by (*i*) measuring the length along the longest axis of the habitat, (*ii*) dividing the length evenly into three perpendicular transects, and (*iii*) measuring the width at the midpoint of each transect. Area (m^2) was calculated as the length × average width. Maximum depth was measured with a stadia rod (cm). Temperature was recorded hourly from 1 January 2007 to 31 July 2007 using thermographs (Onset Corp., HOBO Water Temp Pro version 1) installed in backwater and main channel habitats (upstream segment, $N = 7$; middle segment, $N = 3$; downstream and Black Wolf Creek, $N = 1$ each; Fig. 1). We also recorded whether habitats persisted or dried completely by the end of sampling in late July.

Age-0 fishes were sampled throughout spring and early summer in the spawning habitats previously identified. We classified all of our age-0 study specimens as larvae (i.e., finfold present, or had not yet attained the full adult complement of fin spines or rays in all fins; sensu Snyder and Muth 1990) to streamline presentation for the reader, but recognize that a few individuals would be classified as early juveniles under this definition (e.g., central stonerollers > 20 mm standard length; Auer 1982). In deep backwater habitats (>30 cm maximum depth), we used a paired sampling design to compare efficiencies between two common larval fish sampling methods, dip netting and light trapping. First, larvae were sampled at night using quatrefoil-type light traps (design modified from Killgore 1994). Four 4 mm entrance slots allowed larvae to enter an inner chamber that consisted of four 7.5 cm diameter Plexiglas tubes that were 14 cm long. Traps were suspended from a 6 cm thick Styrofoam ring attached to the top of the trap and floated at the water surface. Upon retrieval, trap contents were flushed into the lower part of the trap that consisted of a 1.5 L bowl (Rubbermaid Corp., TakeAlongs) containing two holes covered with a fine mesh screen that allowed water to drain. Larval fishes were attracted using a 15 cm yellow 12 h Cyalume light stick suspended inside the trap (Extreme Glow Corp, 6" Lightstick). Traps were deployed in fixed positions within backwaters at dusk for approximately 2 h. Laboratory experiments indicated that light traps set for 2 h were effective over an area of at least 28 m^2 (Falke et al. 2010*b*), so multiple traps were used in backwaters larger than 28 m^2.

The following day, larvae were collected by two persons using aquarium dip nets (20 cm × 16 cm; 250 µm-mesh) during daytime spawning habitat surveys. Effort was standardized at 15 min of dip netting by each person in each backwater. Channel margin habitats were not deep enough to sample using light traps (i.e., <30 cm maximum depth), so two persons sampled them using dip nets for 5 min of effort each. Captured larval fishes were preserved in 100% ethanol, except for orangethroat darter (*Etheostoma spectabile*) collected by dip netting. Orangethroat darter is a species of special conservation concern in Colorado (CDOW 2007), and was easily identifiable by sight, so they were counted, measured, and released. All other larvae were identified to species in the laboratory, enumerated, and measured for standard length (SL) to the nearest 0.01 mm, using digital calipers.

Data analyses

Comparison of sampling methods

We tested the efficacy of dip netting vs. light trapping in backwater habitats using paired sample data, with the overall goal of comparing sampling selectivity between the two methods. Specifically, we determined whether, (*i*) one method captured larvae more often than the other, regardless of species; (*ii*) one method consistently captured a species and the other did not (i.e., species selectivity); (*iii*) the length structure within a species differed between the two methods (i.e., size selectivity); and (*iv*) relative abundance indices (measured as catch-per-unit-effort) differed between methods.

Phenology

We used an inverse prediction procedure (Zar 1996) to estimate the initial date of hatching and develop a phenology for larval fishes in the Arikaree River. For each weekly sample, we calculated the 90th percentile SL for each species. We assumed that the largest individuals collected in each week represented the oldest cohort. The single largest fish in each sample was not used because this individual may represent an outlier. We then fit linear regression models of the 90th percentile SL as a function of capture date for each species. We determined the mean SL at hatching for each species from published literature, and then rearranged the linear regression model for each species to solve for the date that corresponded to this estimated mean length at hatching. We also calculated the standard deviation for our point estimates of hatching date (Zar 1996). We considered the endpoint of spawning for each species to be the week in which we last collected larvae within 1 mm SL of their respective mean hatching length.

We compared these estimates of hatching date and hatching duration for each species with continuous data on environmental conditions that might cue spawning. Photoperiod was calculated as the number of minutes of daylight, starting 1 January 2007 (NOAA 2008). We characterized the thermal regime by both the average daily temperature across our 11 thermographs, and cumulatively as growing season degree-days (GSDD) based on those same data. The GSDD were calculated by summing the average daily temperature (°C) from 1 January 2007 to the estimated hatching date for each species. Additionally, we compared initial hatching dates with patterns in groundwater stage and stream flow. Because of the strong influence of groundwater on stream flows in the Arikaree, groundwater table level is an accurate proxy for river stage in this system (Falke et al. 2010*a*). We plotted the mean daily alluvial groundwater table level over time (m; above sea level) from six monitoring wells located in the upstream segment (see Falke et al. 2010*b* for details), and mean daily discharge (m^3·s^{-1}) from US Geological Survey (USGS) gauge No. 6821500 located at the downstream end of the Arikaree River.

Occupancy estimation and modeling

We fit multiple state occupancy models to data for each species to evaluate factors (habitat type and environmental characteristics) that were likely to influence the occurrence and relative abundance state of fish larvae. We also simultaneously modeled the influence of habitat depth and larval size (time) on species detection probability (i.e., detectability).

Using the single-season multiple-state occupancy model described by Nichols et al. (2007), observations for each species were classified into three states: non-detection, 0; low abundance, 1; or high abundance, 2 (see below for criteria). Using these data we estimated the following: the probability that spawning habitat *i* was occupied by larvae (ψ_i^1); the probability that larvae occurred at high abundance given occupancy (ψ_i^2); the probability of detecting the target species in habitat *i* during week *t*, given that the habitat was occupied at low (ρ_{it}^1) or high abundance(ρ_{it}^2); and the probability that high abundances of larvae were found in habitat *i*, during week *t*, given that high abundances of larvae occurred during the season (δ_{it}). The unconditional probability that a habitat was occupied at high abundance was $\psi_i^{1\times2} = \psi_i^1\psi_i^2$ (Nichols et al. 2007).

Counts of larvae observed during each visit to spawning habitats were used to classify detections as follows. First, for each species, we calculated catch-per-unit effort $(c/f)_{it}$ as the number of fish collected (*c*) per minute (*f*) in each habitat *i* during each week *t*. Because estimates of relative abundance were similar between the two sampling methods (see Results) in habitats where both dip netting and light trapping were conducted, $(c/f)_{it}$ were pooled for both methods for occupancy analyses. We reasoned that pooling data from the two sampling methods would improve occupancy estimates, especially for the rare sampling occasions where a species was detected with one method but not the other. Next, to classify species detection into low or high abundance categories, we plotted the frequency of c/f_{it} for each species to look for natural groupings. Distributions for all species were right-skewed, indicating that larvae were often observed at low relative abundance, but occasionally high counts of larvae were detected. We classified a species as being observed at low abundance when c/f_{it} was < 1.0, and high abundance if ≥ 1.0. Across species, this resulted in a mean proportion of 0.85 (±0.03 SE) of (nonzero) observations being classified as low abundance (state 1), and the remaining 0.15 (±0.03 SE) being classified as high abundance (state 2).

Model assumptions

An assumption of occupancy modeling is that sites are closed to changes in occupancy during the survey period or "season" (MacKenzie et al. 2006). We defined the season for each species as the period in which we expected larvae to be present in a habitat, potentially at high abundance. For a given species, we reasoned that the season began on the date we estimated that hatching began (see Results), and extended until habitat shifts due to ontogeny, or high mortality due to increasingly unsuitable environmental conditions (i.e., drying), caused local extinction or reduced the relative abundance state from high to low in spawning habitats. The length of the season varied from 3 to 6 weeks among species. An example detection history for habitat i, h_i = 01221, indicates the site was sampled for five consecutive weeks: the target species was not detected during week 1, but was detected at low abundance during weeks 2 and 5, and at high abundance in weeks 3 and 4. Importantly, the potential for state misclassification extends in only one direction (Nichols et al. 2007). For a site where the target species was not detected (e.g., h_i = 00000), possible occupancy states include unoccupied (true state = 0), occupied at low abundance (true state = 1), or occupied at high abundance (true state = 2). Possible occupancy states for a site where the species was detected at low abundance (e.g., h_i = 10100, observed state = 1), are occupied at low or high abundance, true states 1 and 2, respectively. We assumed that if a species was detected at high abundance (i.e., state 2 was observed during at least one visit) there was no state uncertainty (i.e., true abundance state at the site could not be 0 or 1). In the example detection history h_i = 01221, there is no uncertainty about true abundance state (observed state = true state = 2). As a result, the greatest state uncertainty exists for habitats where no larvae were detected because all three occupancy states are possible.

Habitat covariates

We modeled the probability of occupancy, ψ_i^1, and the probability of high abundance given species occurrence, ψ_i^2, based on the characteristics of individual spawning habitats i at two spatial scales, local and segment. Local scale covariates included habitat area (Area), depth (Depth), a quadratic version of depth (Depth^2), and habitat type (backwater or channel margin). We included the quadratic depth term to assess whether probability of occupancy or high abundance was greatest at a moderate depth. This might be the case if adults avoided spawning in habitats that were too shallow and provided only poor habitat, or too deep and had high predation risk. Segment scale covariates included the segment in which the habitat was located (Segment), stream reach water temperature (GSDD), and persistence of the habitat (Pers). The GSDD was the cumulative number of GSDD (see above) for the reach in which the spawning habitat was located, from 1 January 2007 to the end of the last week of sampling (31 July 2007). We suspected that the probability of high larval abundances for some species might be influenced by thermal characteristics at the reach scale. Finally, we classified each habitat i as to whether the reach within which it was located became intermittent (i.e., no stream flow among habitats) by the end of our spawning habitat surveys (Pers = 0) or not (Pers = 1). Although no reaches dried completely within the period we modeled for any species, many dried by the end of our surveys in July (Falke et al. 2010*a*). Therefore, including this variable might potentially explain the avoidance of particular reaches by individual species, because adults or larvae might demonstrate some ability to choose habitats that are more likely to remain wet during the spawning and rearing period.

Model structure and model selection

Our primary interest was in how the local and segment scale factors (above) influenced occupancy probabilities. Therefore, we kept detection probabilities general, p_{it}^s, allowing them to vary over time (weeks, $t = 1, 2, \ldots T$), abundance state (s = 1, 2), and among locations based on the depth of the individual spawning habitat i ($i = 1, 2, \ldots N$) under the hypothesis that detectability might be lower in deeper habitats. In other words, we expected species detection probability to vary based on time (i.e., as larvae grow, their detection probability changes) and depth (i.e., larvae are harder to detect in deeper habitats). We also expected this effect to be consistent (i.e., have the same slope) for sites with low and high abundance, but the probability could be slightly higher for those sites that support a higher abundance of larvae. As a result, detection probabilities were allowed to differ among low (s = 1) and high (s = 2) abundance-state habitats, but we modeled the effect as consistent (additive) across time and locations:

$$\begin{aligned}\text{logit}(P_{it}^s) &= \beta_0 + \beta_1(\text{state}) \\ &\quad + \beta_2(\text{depth}_i) + \beta_3(t = 2) + \beta_4(t = 3) + \ldots\end{aligned}$$

We also developed a second detection probability structure where depth was not included, p_t^s. We modeled the probability of observing $(c/f)_{it}$ > 1.0 at high abundance habitats as time-specific across weeks, δ_t. Based on the results of our top models, we compared our estimates of p_t^1 or p_{it}^s to the mean size of larvae collected during week t to investigate the relationship between detectability and larval size. We chose to not explicitly model larval size and time as separate covariates on detection because larvae grew linearly over time (see Results). Therefore, we expected the two predictors to covary, preventing any differentiation.

Using these detection probability structures, we developed 11 a priori candidate models that contained sets of explanatory variables (covariates) that were biologically relevant (Table 1). Covariates were used to model both ψ_i^1 and ψ_i^2 simultaneously; we never developed a model where these parameters were functions of different covariates. We included models where ψ_i^1 and ψ_i^2 were a function of local scale covariates (M1–M5), of segment scale covariates (M6, M7), and combinations of local and segment scale covariates (M8, M9). We also constructed a null model (M0), where ψ_i^1 and ψ_i^2 were constant across all habitats, and a global model that included all covariates (MG). We com-

Table 1. Candidate multiple-state models used to estimate occupancy and detectability of larval fishes in spawning habitats in the Arikaree River, Colorado, in 2007.

Model type	Model name	Occupancy covariates						
Global	MG	Area	Depth	Depth^2	Habitat	GSDD	Segment	Pers
Null	M0							
Local	M1	Area						
	M2	Depth						
	M3	Depth	Depth^2					
	M4	Habitat						
	M5	Area	Depth	Habitat				
Segment	M6	Segment						
	M7	GSDD	Segment	Pers				
Mixture	M8	Area	Depth	Habitat	GSDD	Segment	Pers	
	M9	Habitat	Segment					

Note: Models were formulated to address hypotheses at two spatial scales (Local and Segment), separately and in combinations (Mixture). Models were fit with the covariates for occupancy, and with and without one covariate for detectability, which was allowed to vary over time. GSDD, growing season degree days; Pers, persistence of the habitat.

bined these 11 occupancy probability structures with our two detection and classification probability structures to form 22 candidate models, which we fit to our detection data for each species.

We then used an information-theoretic approach to find the most parsimonious set of independent variables to estimate multi-state occupancy and detection probabilities for each species (Burnham and Anderson 2002). We used Akaike's information criterion (AIC) to select the best approximating models by comparing candidate models. The AIC values were adjusted for small sample size (AIC_c), and Akaike weights (w_i) were calculated. The model with the lowest AIC_c and the highest w_i was considered the top model. Because model uncertainty existed, we also drew additional inference from other models with $w_i > 0.05$. All analyses were conducted using the multiple state occupancy estimation model (Nichols et al. 2007) in Program MARK (White and Burnham 1999).

Results

We collected a total of 11 433 fish larvae, representing eight species, from 45 spawning habitats sampled across the three Arikaree River segments and Black Wolf Creek (Table 2). Brassy minnow (*Hybognathus hankinsoni*; 36%) and fathead minnow (*Pimephales promelas*; 31%) dominated the samples, followed by central stoneroller (*Campostoma anomalum*; 13%), northern plains killifish (*Fundulus kansae*; 10%), creek chub (*Semotilus atromaculatus*; 5%), and orangethroat darter (1%). White suckers (*Catostomus commersonii*) were rare, with only eight individuals captured. Green sunfish (*Lepomis cyanellus*; 4%) was only collected during the last week of sampling. As a result, we excluded green sunfish from our phenology and occupancy analyses, and white sucker from all further analyses.

Comparison of sampling methods

The paired comparison of dip netting and light trapping in backwater habitats across 6 weeks in spring 2007 showed that the two methods produced similar results when sampling larval fish communities in Great Plains' stream habitats, although dip netting captured many more larvae than light trapping (N = 9940 vs. 1493, respectively). Of the 64 paired samples, only 14 showed an inconsistency between the two methods in capturing larval fish, regardless of species. In six samples larval fish were collected with dip nets but not light traps, whereas in eight samples larvae were collected with light traps but not dip nets (all eight were during the first week of sampling in early April when larvae were small). Species making up > 5% of the total abundance of larvae during the 6 week period of method comparison included central stoneroller, brassy minnow, fathead minnow, creek chub, and green sunfish. Eighty-five percent of green sunfish larvae were collected using light traps, and most were captured in one backwater during one night, so this species was excluded from further method comparison analyses. Overall, both methods performed well in capturing larval fishes in backwater habitats in the Arikaree River.

We tested species selectivity by calculating the number of samples in which the remaining five abundant species were collected using each method, and analyzed these using a χ^2 test for independence. Based on our results we failed to reject the null hypothesis that the samples were independent ($X^2_{[5]} = 1.23$, $P = 0.87$), which indicated that there was no systematic selectivity whereby one method consistently collected species more often than the other. Likewise, rank abundance of species captured by the two methods was highly correlated ($r_{S[4]} = 0.81$, $P = 0.015$, by Spearman's rank correlation). These analyses indicate that the two methods performed similarly in capturing larval fishes in backwater habitats.

Size selectivity between the two methods was tested for four species for which adequate length-frequency data were available. Five weeks were included in the analysis for brassy minnow, four for central stoneroller and fathead minnow, and one week for creek chub. We tested for equality of the shape of the length-frequency distributions and medians of the distributions for each species between the two methods using two-sample Kolmogorov–Smirnov and Mann–Whitney U tests, respectively. There were no significant differences for the shape or the medians of the length-frequency distributions for any species in any week (all $P >$ 0.13). Therefore, no size selectivity was detected between the two methods for the four most common species collected during the 6 week comparison period.

Table 2. Number of larval fish collected, by species, and number of spawning habitats of each type sampled in each segment in the Arikaree River basin, Colorado, during spring and summer 2007.

	Upstream	Middle	Downstream	Black Wolf Creek
Species				
Central stoneroller	416	826	154	79
White sucker	8	0	0	0
Orangethroat darter	62	22	2	0
Plains killifish	0	562	557	10
Brassy minnow	1393	2166	151	436
Green sunfish	7	433	0	2
Fathead minnow	507	1327	742	970
Creek chub	218	359	24	10
Habitat type				
Backwater	9	5	0	0
Channel margin	5	14	7	5

Finally, we compared the catch-per-unit effort (*c/f*; number of fish·min^{-1}) estimated using the two methods for each species. We calculated the *c/f* for each species in each paired dip net and light trap sample and used linear regression to model the relationship between the two. We found a significant, positive linear relationship ($r = 0.73$, $P = 0.003$) between the *c/f* of species collected using dip netting and light trapping during the same sampling period. This suggested that across species the relative abundances of larval fishes captured were correlated among methods (i.e., many larvae of a species were collected using dip nets when many were collected using light traps). Therefore, because the same effort was used for each method on each sampling occasion, we summed the *c/f* for each species collected in paired dip net and light trap samples as an overall estimate of *c/f* (number of fish·min^{-1}) for individual samples collected in backwater habitats.

Phenology and environmental cues

The six most common fish species in the Arikaree River began spawning at distinct times during spring. Within species, no differences in the relationship of length with capture date were detected among segments (analysis of covariance, ANCOVA, all $P > 0.36$), so we combined estimates across segments for each species. Therefore, our phenology characterizes the fish assemblage in the Arikaree River basin as a whole (Table 3). Size at hatching for each species was estimated from published literature, except for brassy minnow, which was quantified in the laboratory during otolith microstructure validation (Falke et al. 2010*b*). We estimated that the first species to hatch was orangethroat darter, starting 17 April (SD = 4.0 days; Fig. 2). Fish within 1 mm of hatching size (5.0 mm SL; Simon and Wallus 2006) were collected through 23 May, indicating a spawning period of about one month for this species. Creek chub began hatching 19 April (SD = 6.7 days), and spawned through 16 May. Central stoneroller and brassy minnow had similar initial (24 April, SD = 1.7 days, and 25 April, SD = 4.8 days, respectively) and final (23 May) hatching date estimates. Fathead minnow had the longest period of spawning, with hatching estimated to have begun on 30 April (SD = 7.4 days) and lasted through the end of sampling in mid-July. Northern plains killifish was the last species to initiate spawning, not starting until 10 May (SD = 4.7 days) and ending about 13 June. Overall, the spawning period of all six species overlapped for at least a week. Orangethroat darter and creek chub overlapped almost entirely, and central stoneroller and brassy minnow had nearly identical spawning periods. The order of appearance of larvae in samples from 2007 was similar to that observed in 2005 and 2006 (J. Falke, unpublished data). Clearly, mid-April through early June is a critical spawning period for fishes in the Arikaree River.

We investigated the relationship between our estimates of hatching initiation for the six species, and environmental factors that might serve as cues to spawning (Fig. 2). Other than northern plains killifish, which initiated hatching after a spike in discharge and groundwater table level in late April, no other species appeared to be cued by stream flows. Instead, of the factors we measured, photoperiod and water temperatures appeared most likely to initiate spawning in the other five species. Orangethroat darter and creek chub were early season spawners, and initiated spawning at < 600 GSDD (Table 2). Intermediate season spawners were central stoneroller, brassy minnow, and fathead minnow, which initiated spawning between 660 and 740 GSDD. Northern plains killifish, the latest species to spawn in the Arikaree River, did not initiate spawning until after about 900 GSDD.

Larval occupancy, relative abundance, and spawning–habitat relationships

The probability that a spawning habitat was occupied by larvae, regardless of abundance state ($\hat{\psi}^1$), varied from 0.62 (±0.08 SE) for northern plains killifish, to 0.94 (±0.29 SE) for central stoneroller (Table 4). The unconditional probability that a spawning habitat was occupied by larvae at high abundance ($\hat{\psi}^{1\times2}$) ranged from 0.23 (±0.06 SE) for northern plains killifish to 0.65 (±0.07 SE) for central stoneroller. Four of the six species had high probabilities of occupancy ($\hat{\psi}^1$; 0.82–0.95), but were found at high abundance in only about half of the habitats ($\hat{\psi}^2$; 0.49–0.65), whereas the other two species had lower probabilities of occupancy, and occupancy at high abundance. After accounting for imperfect detection, modeled estimates of the probabilities of occupancy

Table 3. Estimates of the initiation of hatching for six fish species collected in the Arikaree River, Colorado, during spring 2007.

	Model						
Species	r^2	β_0	β_1	Hatching initiation	GSDD	Hatching size (mm)	Reference
Orangethroat darter	0.97	108 (4.0)	0.22	17 April	571	5.0	Simon and Wallus (2006)
Creek chub	0.97	110 (6.7)	0.38	19 April	595	5.8	Buynak and Mohr (1979)
Central stoneroller	0.99	115 (1.7)	0.52	24 April	662	5.7	Reed (1958); Buynak and Mohr (1980)
Brassy minnow	0.96	116 (4.8)	0.40	25 April	671	4.0	Falke (2009)
Fathead minnow	0.96	121 (7.4)	0.33	30 April	741	3.6	Snyder et al. (1977)
Plains killifish	0.94	131 (4.7)	0.33	10 May	893	5.7	Koster (1948)

Note: Coefficients of determination (r^2), *x*-axis intercepts (β_0) and standard deviation in parentheses, the slope (β_1) of each model, the estimated hatching date, growing season degree days (GSDD; cumulative °C) for that date, and the size at hatching (mm) based on published literature are presented.

Fig. 2. Spawning phenology for six Great Plains fish species in the Arikaree River, Colorado. Top panel (*a*) is the date of hatching initiation for each species (error bars are 1 SD), and the estimated duration of hatching. In the middle panel (*b*) are mean water temperature collected across 12 thermographs (broken line) and cumulative photoperiod (minutes of daylight; unbroken line). Lower panel (*c*) is the mean alluvial groundwater table level (groundwater stage) collected across six wells in the upstream segment (m above sea level; unbroken line), and daily discharge from USGS gauge 6821500 ($m^3 \cdot s^{-1}$; broken line). All data are from 2007.

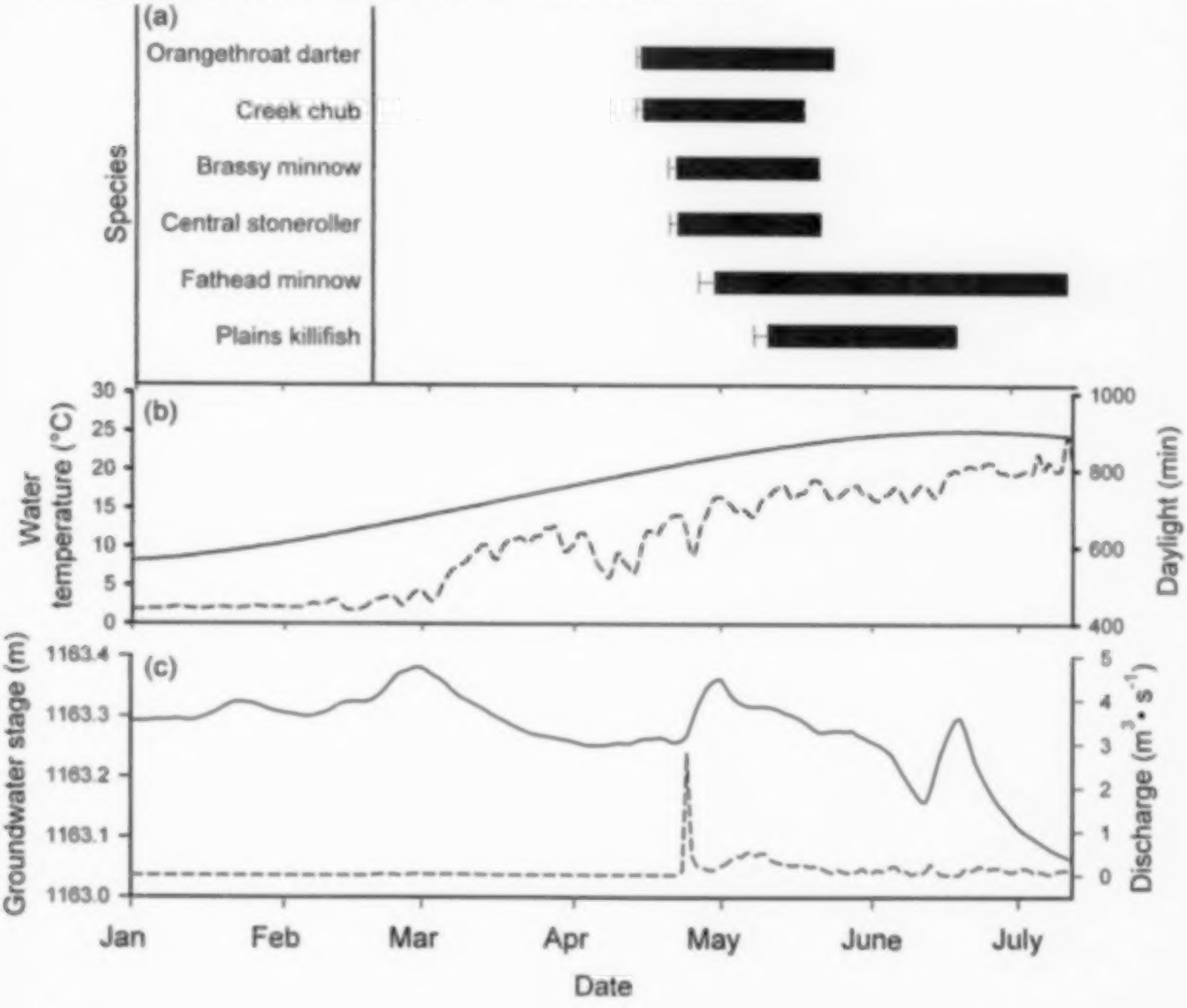


Table 4. Naive and model-based estimates of occupancy and detectability of fish larvae collected from 45 spawning habitats in the Arikaree River, Colorado.

		Naive occupancy			Modeled occupancy			Detectability
Species	No. weeks	$\tilde{\psi}^1$	$\tilde{\psi}^2$	$\tilde{\psi}^{1\times2}$	$\hat{\psi}^1$	$\hat{\psi}^2$	$\hat{\psi}^{1\times2}$	p_t^1
Central stoneroller	5	0.76	0.62	0.47	0.94 (0.29)	0.69 (0.22)	0.65 (0.07)	0.33–0.89
Orangethroat darter	6	0.47	0.22	0.10	0.63 (0.16)	0.51 (0.12)	0.42 (0.16)	0.14–0.73
Plains killifish	3	0.60	0.22	0.13	0.62 (0.08)	0.37 (0.10)	0.23 (0.06)	0.72–0.93
Brassy minnow	5	0.87	0.47	0.40	0.89 (0.05)	0.57 (0.09)	0.50 (0.08)	0.73–0.95
Fathead minnow	5	0.91	0.44	0.40	0.93 (0.04)	0.53 (0.09)	0.49 (0.09)	0.06–0.88
Creek chub	4	0.80	0.56	0.44	0.82 (0.04)	0.65 (0.09)	0.53 (0.15)	0.05–0.71

Note: Number of weeks modeled, occupancy estimates based on raw data (naive), and multiple-state occupancy models are presented. Estimates are reported at mean covariate values from top models based on AIC$_c$, and standard errors of model estimates are in parentheses. Detectability is the range of detection probabilities observed over time.

and high abundance were often substantially higher than naive estimates (i.e., the number of habitats where a species was captured / the total number of habitats) of those parameters.

Multi-state occupancy models included only local-scale covariates (habitat area, depth, and (or) type) for all six species except northern plains killifish and fathead minnow, indicating that these characteristics provided the best description of occupancy states for these species, given the data (Table 5). Occupancy states of northern plains killifish were best explained by a mixture of local (e.g., habitat type) and segment scale covariates. The best supported model for creek chub was the null model (no covariates on occupancy), although there was some support for models indicating that this species had higher probabilities of occurrence and conditional high abundance in small, deep habitats.

Habitat area or depth, and habitat type (i.e., backwater or channel margin) were present in the top three models for four of the six species (Table 5). Probabilities of occurrence and conditional high abundance for central stoneroller were higher in relatively large, shallow, channel margin habitats, whereas orangethroat darter tended to occupy similar, but smaller, habitats. Conversely, brassy minnow occupancy and conditional high abundance probabilities were highest in large, deep, backwater habitats. Segment was an important predictor of the probability of conditional high abundance for northern plains killifish and fathead minnow. Larvae of these two species were most likely to be found in the middle and downstream segments. Overall, the direction of effects and covariates contained in the top models differed among species, indicating that larval occurrence and relative abundance for each species in spawning habitats were influenced by different attributes. Although some model uncertainty existed, this was a higher level of spawning habitat specialization than we predicted, based on general habitat preferences of adults during summer and winter (Falke and Fausch 2010).

Spawning habitat area influenced the probability of conditional high abundance for several species, although the direction of effects differed (Table 5; Fig. 3). For example, brassy minnow larvae were more likely to occur at high abundance in larger spawning habitats. We predicted a 50% probability of conditional high abundance of brassy minnow larvae in backwaters with areas of approximately 25 m^2. The probability of conditional high abundance of central stoneroller larvae in spawning habitats also increased with spawning habitat area, although the slope of the relationship was more gradual than for brassy minnow. Conversely, the probability of conditional high abundance of orangethroat darter and creek chub larvae declined with area, indicating that adults of these species preferred to spawn in smaller habitats. Overall, habitat size was an important predictor of larval occurrence and relative abundance states.

Our ability to detect larvae in spawning habitats with low abundances (p_t^1) varied considerably among species and over time (Table 4). Creek chub had the lowest single probability of detection in low abundance habitats (p^1 = 0.05), which occurred during week 6, whereas brassy minnow had the highest (p^1 = 0.95), occurring during week 7. Fathead minnow and creek chub had the greatest range of p_t^1 estimates, whereas values for northern plains killifish and brassy minnow were consistently high (≥0.72). Maximum estimates of p_t^1 were > 0.70 across species, indicating that all six can be efficiently detected during at least one week. Detectability was even higher for all species when they occupied habitats at high abundance.

Detectability of central stoneroller and orangethroat darter was lowest early in the spawning season, when larvae were very small; and late in the spawning season, when larvae were large, thus matching our predictions (Fig. 4). However, detectability of northern plains killifish, brassy minnow, and fathead minnow generally increased and remained high, indicating that small larvae of those species were more difficult to detect, but larger larvae were not. Detectability of creek chub larvae was highest early in the sampling period and declined rapidly thereafter, corresponding to the period when larger individuals were present.

Detectability for three of the six species (central stoneroller, brassy minnow, and fathead minnow; Table 5; Fig. 5) declined with increasing spawning habitat depth. The probability of detecting central stoneroller larvae declined rapidly at depths > 60 cm, whereas detectability of brassy minnow and fathead minnow larvae remained high (>70%) in habitats as deep as 70 cm. Depth did not influence detectability of orangethroat darter, northern plains killifish, or creek chub, in large part because these fish spawned in shallow habitats (Fig. 3).

Table 5. Results of multiple-state occupancy models for larvae of six species of Great Plains stream fish in the Arikaree River in 2007.

	Occupancy										
	Local scale			Segment scale			Detection	Model results			
Model	Area	Depth	Habitat	GSDD	Segment	Persistence	Depth	K	AIC$_c$	ΔAIC$_c$	w_i
Central stoneroller											
M5	(+)	(–)	(CM)				(–)	20	310.69	0.00	0.76
M1	(+)						(–)	16	313.52	2.83	0.18
M4			(CM)				(–)	16	317.38	6.69	0.03
MG								30	415.04	109.89	<0.01
Orangethroat darter											
M2		(–)						17	225.79	0.00	0.63
M1	(–)							17	228.51	2.71	0.16
M4			(CM)					17	229.04	3.32	0.12
MG								30	360.75	134.95	<0.01
Plains killifish											
M4			(CM)		(MS)(DS)			15	180.79	0.00	0.63
M7				(+)	(MS)(DS)	(DRY)		17	182.86	2.07	0.22
M6					(MS)(DS)			14	184.68	3.89	0.09
MG								30	250.74	69.94	<0.01
Brassy minnow											
M1	(+)						(–)	16	360.2	0.00	0.60
M4			(BW)				(–)	16	361.68	1.47	0.31
M2		(+)					(–)	16	365.96	5.76	0.06
MG								30	466.52	106.32	<0.01
Fathead minnow											
M9			(CM)		(MS)		(–)	20	363.71	0.00	0.73
M1	(+)						(–)	16	366.06	2.36	0.22
M4			(CM)				(–)	16	370.14	6.44	0.03
MG								30	462.41	98.71	<0.01
Creek chub											
M0								11	223.81	0.00	0.68
M2		(+)						13	226.09	2.28	0.23
M1	(–)							13	231.50	7.69	0.05
MG								30	288.96	65.15	<0.01

Note: Model results for each species are ranked by AIC$_c$ (w_i, Akaike weight), from best to worst. Direction of effects for each covariate is indicated by + (positive) or – (negative), except for categorical predictors, which were all positive. CM, channel margin habitat; BW, backwater habitat; MS, middle segment; DS, downstream segment; DRY, habitats dried. The global model for each species (MG) is presented for reference. See Table 1 for a description of the models, and the text for parameter descriptions.

Discussion

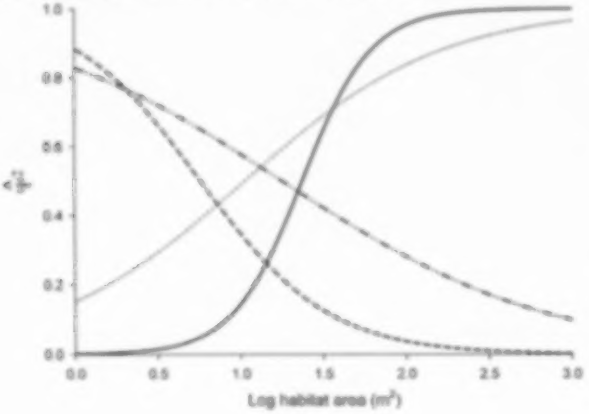
Continued anthropogenic degradation of Great Plains streams will undoubtedly influence the availability of spawning habitats and the dynamics of fish species that rely on these habitats for successful recruitment. As a result, knowledge of basic life-history attributes, paired with unbiased estimates of patterns in distribution along the riverscape, is critical for effective conservation of sensitive species. In this study, we estimated the initiation of hatching and constructed the spawning phenology for an assemblage of six western Great Plains fish species, and used newly developed multi-state occupancy models to analyze factors that influence the occurrence and abundance state of these species in spawning habitats. Here we discuss our findings on spawning phenology and habitat use, the implications of our results for sampling larval plains fishes, and their application in planning conservation strategies for imperiled Great Plains stream fishes.

Phenology

To our knowledge, our spawning phenology constructed using inverse prediction models is the first for a western Great Plains stream fish community, although there are some data for the southern Great Plains (Durham and Wilde 2005), and dryland streams in Australia (King et al. 2003). We found that all species initiated spawning in spring and had discrete spawning periods, except fathead minnow, which spawned for an extended period. At the level of families, our estimate of the order of spawning was similar to those made in other temperate stream ecosystems (e.g., Floyd et al. 1984), where the order was percids, cyprinids, cyprinodontids, then centrarchids.

We found that estimates made using the inverse prediction models were very similar to estimates made from aging larvae directly from otoliths. For example, our estimate for the initiation of hatching in brassy minnow was 25 April (±4.8 d) using the inverse prediction models, and the first

Fig. 3. Conditional probability of occupancy at high abundance (ψ_i^2) of larvae of four Great Plains fish species across 45 spawning habitats in the Arikaree River, Colorado, in 2007, as a function of spawning habitat area (m^2). Lines represent brassy minnow (unbroken line), central stoneroller (dotted line), orangethroat darter (broken line), and creek chub (broken-dotted line).



date of hatching from daily ring counts was estimated to be 21 April (Falke et al. 2010*b*). As a result, if size at hatching is known for a species, and samples are collected over multiple site visits, the inverse prediction method may be quite useful in estimating the initiation of hatching. This method requires less effort and expert knowledge than the fine art of extracting and reading daily increments in otoliths.

Relative to the other factors we measured, discharge did not appear to be correlated with initiating spawning for five of the six species we analyzed. This is not surprising because species that are known to be influenced by flow spikes (e.g., plains minnow *Hybognathus placitus*; Taylor and Miller 1990) are already extirpated from the Arikaree River owing to declines in stream flow from pumping groundwater for irrigation (Falke 2009). Instead, the initiation of hatching for most species appeared to be influenced by rising water temperatures from winter to spring. Our results agree with those of Falke et al. (2010*b*), where brassy minnow were found to spawn earlier under a warmer thermal regime. In Great Plains streams such as the Arikaree River, water temperatures are controlled by interactions among climate, geomorphology, and groundwater input. Spawning habitats (i.e., backwaters) are often well connected to alluvial aquifers, resulting in relatively benign environmental conditions. As groundwater levels continue to decline due to irrigation pumping (Falke et al. 2010*a*), habitats are likely to warm faster, causing fishes to spawn sooner. If so, we predict that premature spawning, and a potentially contracted spawning season due to climate change, will reduce recruitment through decreased per capita production of larvae, as well as lowered survival of offspring.

Spawning habitat use

Local-scale spawning habitat characteristics influenced both occupancy and relative abundance probabilities of plains fish larvae. Habitat size (i.e., area or depth) and habitat type were the most important factors across species. This specialization was surprising, and was stronger than we expected, given the generalized habitat preferences of adult plains fishes during other parts of the year (Taylor et al. 1993; Falke and Fausch 2010). This finding underscores the importance of movement by plains stream fishes to use habitats that are dispersed throughout the riverscape (Labbe and Fausch 2000; Scheurer et al. 2003), and the need to conserve all habitat types (e.g., spawning, rearing, and refuge) they require to carry out their life histories (Fausch et al. 2002). For example, we found that brassy minnow required large, deep, backwater habitats for successful spawning. These results indicate that there may be a threshold of habitat size for successful spawning by these species.

Interestingly, we found that the probability that larvae occupied habitats (ψ_i^1) was relatively high, regardless of species. In other words, larvae of most species occurred in most spawning habitats, but often at low abundance. However, the probability of high relative abundance (conditional on occupancy), which we associated with spawning habitat preference by adults, was considerably lower. These results suggest that although adults were choosing among different habitat types (e.g., backwater or channel margin) for spawning; once hatched, larvae may move or be moved from natal habitats. Likely mechanisms for this phenomenon are (*i*) passive dispersal of larvae during high flow events, (*ii*) ontogenic habitat shifts (i.e., larvae hatch in backwaters but move to channel margins at a certain size; Falke et al. 2010*b*), or (*iii*) the species is a generalist with regard to spawning habitat preference. For example, we found that habitat type was not an important predictor of the probability of occupying spawning habitats at high abundance for creek chub. However, for brassy minnow, all three mechanisms may be important, and may change through ontogeny (Falke et al. 2010*b*).

Larval fish sampling and detectability

Overall, we detected no differences in the species of larval fish captured, their size distribution, or their relative abundance (*c*/*f*) between dip netting and light trapping. This suggests that both methods allow robust measures of presence and relative abundance of larval fishes in plains streams like the one we sampled. However, nearly an order of magnitude more individuals were collected using dip nets versus light traps. If large sample sizes are needed for analyses, dip netting would be a superior method for sampling larval fishes in plains stream habitats. Conversely, if negative impacts to population levels (e.g., rare species) from sampling are a concern, then light trapping may be a better alternative.

Using observations of relative abundance (*c*/*f*) to define two relative abundance states, we were able to produce unbiased estimates of three occupancy states for larvae of six species of plains fishes in spawning habitats, based on multiple site visits. These estimates accounted for imperfect detection, which is rarely incorporated into studies of larval fish ecology. To our knowledge, these are the first estimates of the influence of fish size (time) and habitat characteristics on detectability of fish larvae in streams. Specifically, we found that habitat depth and time influenced the probability of detection of larvae in spawning habitats, and that detect-

Fig. 4. Probability of detection of larvae of six plains fish species (circles; left y-axis) and mean standard length (mm; triangles; right y-axis) in spawning habitats in the Arikaree River, Colorado, across 6 weeks of sampling during late spring to early summer 2007. Estimates are from top models ranked using AIC$_c$.

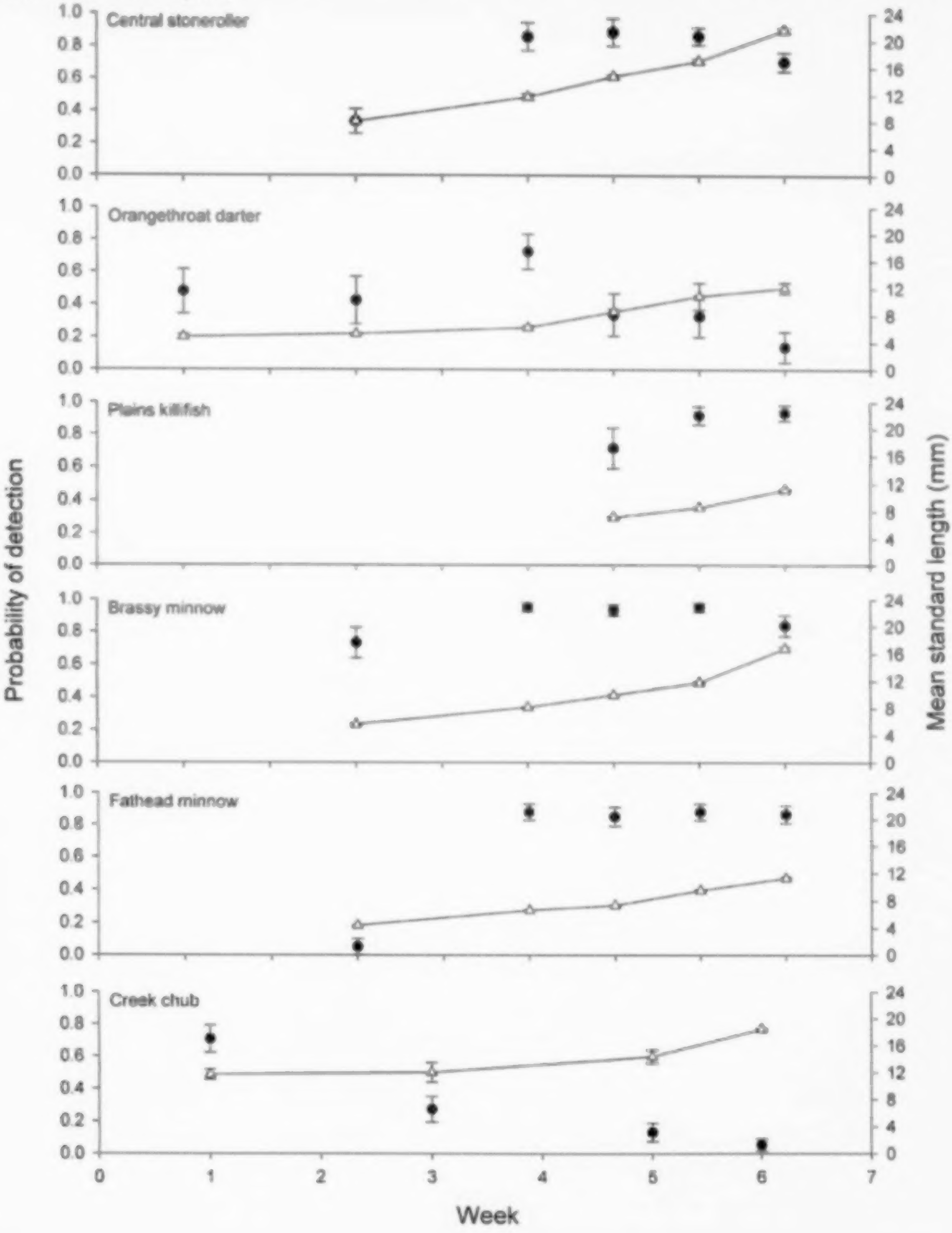
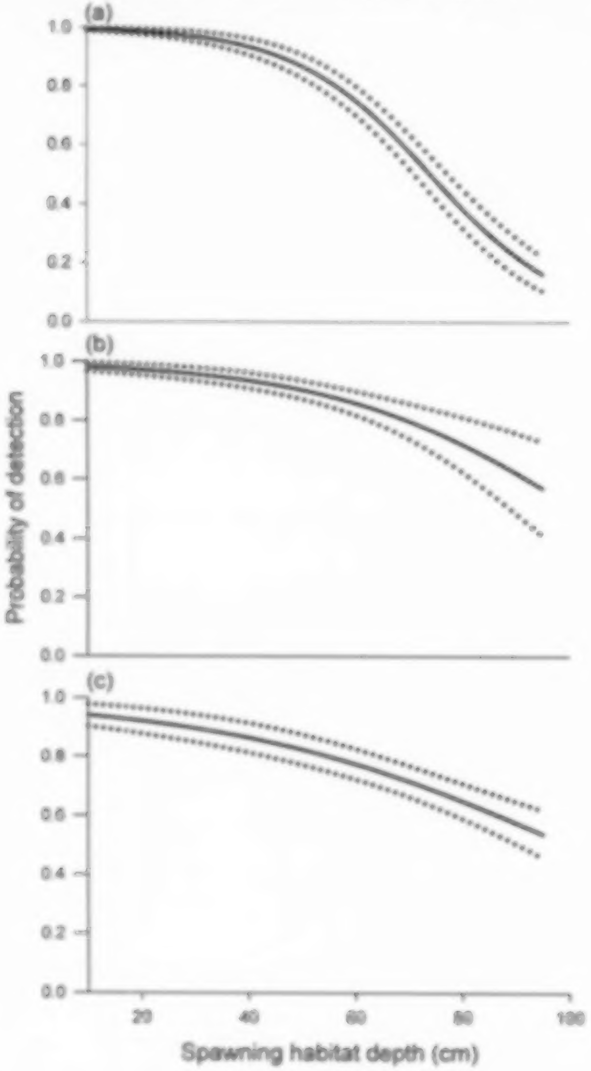


Fig. 5. Overall probability of detection of larvae of central stoneroller (*a*), brassy minnow (*b*), and fathead minnow (*c*) as a function of spawning habitat depth. Dotted lines represent 90% confidence intervals. Estimates are from top models ranked using AIC.



ability was heterogeneous among species. Detectability was never perfect (i.e., probability = 1), nor did it peak during the same week among species. For example, the highest detectability of creek chub larvae was early in the sampling period, whereas the highest probability of detecting northern plains killifish larvae was late in the sampling period. This indicates that to accurately quantify the occupancy state of larvae at the assemblage level, multiple site visits over time are needed. In addition, even if the species was detected, the appropriate abundance state was not always observed (i.e., $\delta_{ij} < 1$), suggesting that if investigators want to differentiate between multiple occupied states, several visits are necessary. We found that detectability of three species also declined in deeper habitats. However, detectability of these species remained relatively high (>0.7) across the majority of the range of depths (<70 cm) encountered in spawning habitats in the Arikaree River. Only two spawning habitats sampled were > 70 cm maximum depth. We suggest that sampling effort may need to be adjusted (i.e., increased) in deeper spawning habitats to adequately detect the presence of larvae of central stoneroller, brassy minnow, and fathead minnow.

Our sampling design provided unbiased estimates of occupancy and relative abundance states for an assemblage of Great Plains stream fish larvae, allowing us to critically evaluate two sampling methods, as well as quantify variation in sampling efficiency and detectability for six species. We estimated the spawning phenology of this assemblage, and the influence of spawning habitat characteristics on habitat use and relative abundance of larvae. In the process we gained much insight about the life history of these species that was previously unknown.

Knowledge of spawning initiation and duration, and the environmental factors that serve as cues, is extremely important for species conservation, especially in Great Plains streams where habitat continues to be lost owing to altered flow regimes from water abstraction. In the Arikaree River, unsustainable groundwater pumping for agricultural irrigation had reduced the river to about 10% of its former length by 2007, and further loss of key habitats needed by fishes for spawning, rearing, and refuge is expected to occur into the future (Falke and Fausch 2010; Falke et al. 2010*a*). This hydrologic alteration has led to the loss of 5 of 15 native fish species since the 1950s. Similar patterns of groundwater use, habitat loss, and community change have occurred across the western Great Plains (Eberle 2007; Falke et al. 2010*a*; Gido et al. 2010). Therefore, our work is relevant for sampling and detecting plains fish species as larvae (i.e., when they are most abundant and thus most detectable), as well as measuring habitats where these fishes spawn and rear, to understand their life history and aid in conservation of critical habitats. Future work should integrate current knowledge of spatial and temporal spawning dynamics of imperiled Great Plains stream fishes with physical models of groundwater and pumping to develop realistic plans for species conservation in these rapidly declining stream ecosystems.

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Ecological periodic tables for nekton usage of four US Pacific Northwest estuarine habitats

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Abstract: We compared the species composition and abundance of the total nekton community, using the Bray–Curtis similarity coefficient, and mean total nekton, fish and crab species richness, abundance and biomass, and shrimp abundance across four intertidal habitats in a US Pacific Northwest estuary: (*i*) eelgrass (*Zostera marina*); (*ii*) burrowing mud shrimp (*Upogebia pugettensis*); (*iii*) burrowing ghost shrimp (*Neotrypaea californiensis*); and (*iv*) unvegetated sand. Field sampling was conducted during daytime high tides, and was quantitative, stratified-by-habitat, randomized, and estuary-wide. More than 10 000 nekton specimens belonging to 64 taxa were collected in 454 samples during 10 sampling periods, each approximately one-month-long (from June to November), over 3 years (1998–2000). Non-metric multidimensional scaling analyses revealed annually recurring across-habitat patterns in total nekton Bray–Curtis similarity. Two-way (*habitat*, *year*) analyses of variance revealed annually recurring across-habitat patterns on 10 indicators of nekton-habitat quality and preference. Total nekton species richness, abundance, and biomass were, respectively, on average, 8 ×, 25 ×, and 25× greater in eelgrass, 4 ×, 6 ×, and 5× greater in mud shrimp, and 2 ×, 3 ×, and 2× greater in ghost shrimp, than in sand habitat. Our findings validate the ecological relevance of our habitats to nekton, and suggest they can serve as elements in ecological periodic tables of nekton habitat usage.

Résumé : Nous avons comparé la similarité de Bray–Curtis du necton total, ainsi que la richesse spécifique, l'abondance et la biomasse moyennes du necton total, des poissons et des crabes, de même que l'abondance des crevettes dans quatre habitats intertidaux (à zostère marine (*Zostera marina*), à crevettes fouisseuses des vases (*Upogebia pugettensis*), à crevettes fantômes fouisseuses (*Neotrypaea californiensis*) et de sable sans végétation) dans un estuaire de la côte américaine de la région pacifique du nord-ouest. L'échantillonnage sur le terrain a été fait durant les marées hautes de jour et comportait des échantillons quantitatifs, stratifiés par habitat, aléatoires et couvrant tout l'estuaire. Nous avons récolté plus de 10 000 individus du necton appartenant à 64 taxons dans 454 échantillons durant dix périodes d'échantillonnage d'environ un mois (juin à novembre) sur trois années (1998–2000). Des analyses de cadrage multidimensionnel non métrique montrent des patrons de similarité de Bray–Curtis dans le necton total entre les habitats qui se répètent d'année en année. Des analyses de variance à deux critères de classification (*habitat*, *année*) révèlent des patrons récurrents d'année en année à travers les habitats de dix indicateurs nectoniques de la qualité et de la préférence des habitats. La richesse spécifique, l'abondance et la biomasse du necton total sont en moyenne respectivement 8 ×, 25× et 25× plus grandes dans les habitats à zostère, 4 × , 6× et 5× plus grandes dans les habitats à crevettes des vases et 2 × , 3× et 2× plus grandes dans les habitats à crevettes fantômes que dans les habitats sablonneux. Nos observations confirment la pertinence de nos habitats pour le necton et indiquent qu'ils pourraient servir d'éléments dans des tableaux périodiques écologiques de l'utilisation faite par le necton.

[Traduit par la Rédaction]

Introduction

In his presidential address to the British Ecological Society, Southwood (1977) compared the situation in ecology to that in chemistry before the development of the periodic table of chemical elements when each fact, for example, the solubility or reactivity of a chemical element, had to be discovered independently and remembered in isolation. Southwood (1977) theorized that since ecological strategies evolve from the interaction between the habitat and the organisms, "a sort of ecological periodic table" might be constructed with a set of habitat characters, or habitat templates, as the organizing elements. Information-organizing structures improve the access to and retrieval of information, and can lead to new insights, understanding, and predictive capabilities. The key to the development of the chemical periodic table was in arranging the elements in the table to reflect recurring (periodic) chemical properties (Scerri 2007).

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The periodicity of the chemical properties was discovered primarily by empirical induction (Scerri 2007). A parallel approach to develop ecological periodic tables for nekton habitat usage is to discover recurring empirical relationships between operational definitions of nekton and habitats (Jax 2006; Dodds 2009), and to arrange the elements (habitats) in the table to reflect periodic nekton properties.

We tested for annually recurring habitat usage patterns for nekton across four operationally defined US Pacific Northwest intertidal habitats. Three habitats were characterized by the presence of "ecosystem engineering" (Jones et al. 1994) or "niche constructing" (Boogert et al. 2006) species: (*i*) eelgrass (*Zostera marina*); (*ii*) burrowing mud shrimp (*Upogebia pugettensis*); and (*iii*) burrowing ghost shrimp (*Neotrypaea californiensis*), hereinafter referred to by the genus name alone. The fourth habitat was unvegetated sand, hereinafter, "sand." *Upogebia* and *Neotrypaea* are, respectively, filter-feeding and deposit-feeding burrowing shrimp that change the sediment surface topology and the physiochemical environment (Bird 1982; DeWitt et al. 2004). We suspected that habitat usage for nekton would differ among the four habitats because they differ with respect to the amount of habitat structure [*Zostera* (leaves) > *Upogebia* ≈ *Neotrypaea* (surface mounds and burrow holes) > sand] and benthic macrofaunal prey density (*Zostera* > *Upogebia* > *Neotrypaea* ≈ sand; Bird 1982; Berkenbusch and Rowden 2007; Ferraro and Cole 2007), which are two factors known to affect nekton spatial distributions (Orth et al. 1984; Hemminga and Duarte 2000; Jackson et al. 2001). The four habitats are ecologically and environmentally important because they account for most of the intertidal area of many US Pacific Northwest estuaries (DeWitt et al. 2004; Lee et al. 2007) and they are alternative states (van de Koppel et al. 2001; Ruesink and Trimble 2007) subject to change as a function of the major stressors (Emmett et al. 2000; Borde et al. 2003). We constructed an ecological periodic table showing habitat usage for nekton based on the empirical relationships found between the habitats and nekton indicators of habitat quality and preference, such as species richness, abundance, and biomass (Rozas and Minello 1998), which are also partial indicators of the value of the habitat as a nursery (Beck et al. 2001; Heck et al. 2003; Minello et al. 2003).

Materials and methods

Our study site, Yaquina Bay, Oregon, United States (124°03′W, 44°38′N; Fig. 1) is, like many Oregon coastal estuaries, a small (15.8 km^2), shallow, drowned river valley estuary with tidal flats covering >60% of its area (Bayer 1981; Lee et al. 2007). Yaquina Bay tides are mixed semidiurnal with a mean high tide of ~2.5 m (Kentula and DeWitt 2003). Water temperature and salinity vary with location, tidal stage, rainfall, and season. De Ben et al. (1990) reported mean monthly bottom water temperatures of 7–23 °C and mean monthly salinities of 8‰–28‰ depending upon location. From mid-spring through early fall in lower Yaquina Bay, bottom water temperatures range between 9–17 °C (De Ben et al. 1990) and salinities are typically oceanic (33‰–35‰) (Kentula and DeWitt 2003).

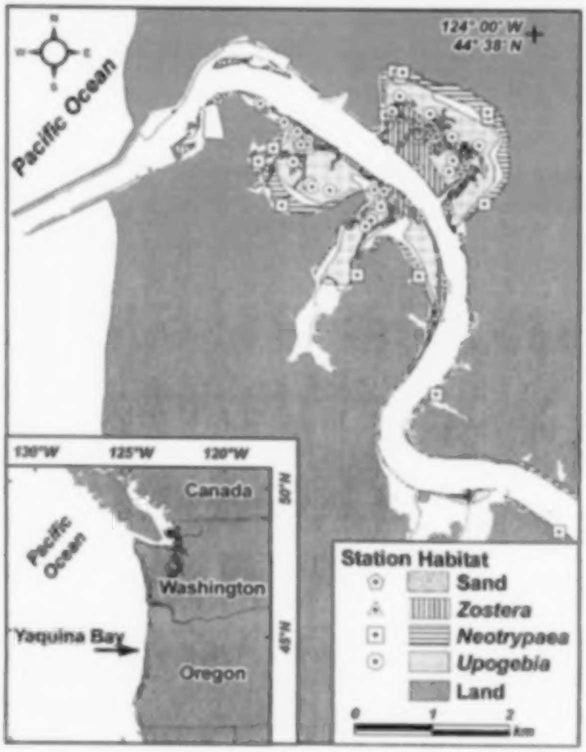
Our field sampling design was stratified-by-habitat, randomized, and estuary-wide. A habitat map was constructed using information on the distribution of *Zostera* (Young et al. 1998), *Upogebia*, *Neotrypaea*, and sand (DeWitt et al. 2004) in Yaquina Bay (Fig. 1). The areas of the four habitats were digitized and entered as data layers in a geographic information system (ESRI ArcView version 3.3). Random (Stevens 1997) field stations (15 in the *Zostera* habitat, 15 in the *Upogebia*, 14 in the *Neotrypaea*, and 11 in the sand habitat) were identified for repeated sampling within each habitat. Fewer random stations were placed in the sand habitat because its total area (0.06 km^2) was much less than that of the other habitats (1.0–2.9 km^2). Field stations were located using a Global Positioning System accurate to 5 m.

Our sampling gear was a cylindrical fiberglass drop sampler 1.8 m high, with 1.8 m^2 surface area, and a 15 cm metal bottom skirt. The drop sampler was extended beyond the bow of our work boat from an I-beam, and dropped to the sea bed as the boat slowly and quietly drifted on station. Our collection protocol was to thoroughly sweep the entire volume of water enclosed by the drop sampler a minimum of 10 times with a large (~0.1 m^2) 3-mm-mesh dip net, taking additional sweeps, as necessary, until the last three sweeps produced no fish or crabs. The nekton collected using this sampling protocol became our operational definition of "the total nekton community" (Jax 2006). A mark-and-recapture study in which 10 marked fish [shiner perch (*Cymatogaster aggregata*) or Pacific staghorn sculpin (*Leptocottus armatus*)] and 10 marked crabs [Dungeness crabs (*Cancer magister*) or yellow shore crabs (*Hemigrapsus oregonensis*)] were added to drop samplers in the field (*n* = 41 trials), indicated a mean (±SE) catch efficiency of 87% (±2.1%) for fish and 67% (±3.3%) for crabs by this method, with no differences in catch efficiency among habitats. Nekton removed from each drop sampler was placed in labeled jars and preserved in 10% formalin.

Nekton samples were collected during daytime high tides, when the water level was ~1 m deep, during two, discrete, approximately month-long sampling periods in 1998 (period 2, 21 July to 22 August; period 3, 1–29 September) and four, discrete, approximately month-long sampling periods (period 1, 15 June to 12 July; periods 2 and 3 the same as for 1998; period 4, 4 October to 2 November) in 1999 and 2000. Three habitats (*Zostera*, *Upogebia*, and *Neotrypaea*) were sampled in 1998, and four habitats (*Zostera*, *Upogebia*, *Neotrypaea*, and sand) were sampled in 1999 and 2000. Winds >15 knots (7.72 m/s) made the deployment of our drop sampler unsafe. The high frequency of windy days in the winter and early spring on the Oregon coast made year-round sampling impractical. High winds and technical problems prevented the collection of samples at all our stations during several of our sampling periods. When possible, we sampled some stations twice (7–28 days apart) during a sampling period to increase the sample size and the statistical power of our tests. As we were unable to sample the same set of random stations in every sampling period, our statistical designs were analysis of variance (ANOVA) and its multivariate analog, analysis of similarities (ANOSIM), not a repeated testing design (Sokal and Rohlf 1995).

Water temperature (±0.5 °C), salinity (±0.5‰), and depth (±1 cm) of sampling for the drop sampler were measured

Fig. 1. Habitat map of Yaquina Bay, Oregon, USA, showing station locations.



and recorded at the time of sampling. At the beginning and end of our study we estimated the percent cover of *Zostera* (Duarte and Kirkman 2001), and estimated the density of *Upogebia* and *Neotrypaea* by counting shrimp burrow holes (Posey 1986) within a 0.25-m^2 quadrat. Five-centimetre deep sediment core samples were collected at each station, and, in the laboratory, the percentage of sand (particles > 0.065 mm), silt (particles 0.0039–0.065 mm), and clay (particles < 0.0039 mm) in the samples was determined by the sieve and pipette method (Buchanan 1984).

The field-collected nekton was transferred to 70% ethanol in the laboratory, and identified to the lowest taxon possible, usually species, and counted. All the fish and crab specimens were measured [fish total length (TL) and crab carapace width (CW); ±1 mm] using calipers, and weighed (±0.01 g, wet weight, (wwt)) on an electronic balance. The total fish and crab biomass in each sample was determined by summing the weights of the individual fish and crabs, respectively. Total nekton biomass in each sample was determined by weighing the other nekton taxa (±0.01 g, wwt) and adding their total weight to the weights of total fish and crabs.

One-way ANOSIM (global *R* test) and habitat pair-wise comparisons (*R* test) were conducted by sampling period to test for across-habitat patterns in total nekton Bray–Curtis similarity (Bray and Curtis 1957) with raw, square-root-transformed data (Clarke and Warwick 2001). The null hypotheses (H_0) stated that there would be no significant (α = 0.05) habitat differences in total nekton species composition and abundance (global *R* test) and no significant (α = 0.05) differences in total nekton species composition and abundance between habitat pairs (*R* test). Rejection of these H_0 for the same sampling period in multiple years implies there were annually recurring (year-over-year, i.e., year-to-year during the same sampling period of the year) across-habitat patterns of differences in total nekton species composition and abundance. Non-metric multidimensional scaling (MDS) plots were generated (Clarke and Warwick 2001) to show the results graphically. Bray–Curtis similarities in MDS plots are adequately represented by distances between samples (samples most similar are closest together, and those least similar are farthest apart) when stress values are < 0.2 (Clarke 1993).

Two-way (*habitat*, *year*) ANOVAs (Sokal and Rohlf 1995) were conducted to test for annually recurring across-habitat patterns on 10 measures of nekton community structure: the mean number of species or lowest identifiable taxon of (*i*) total nekton, (*ii*) fish, and (*iii*) crabs; mean abundance of (*iv*) total nekton, (*v*) fish, (*vi*) crabs, and (*vii*) shrimp; and mean biomass (g, wwt) of (*viii*) total nekton, (*ix*) fish, and (*x*) crabs. Tests were conducted on the form of the data that best met the parametric assumptions (Sokal and Rohlf 1995). These were species richness, $\log_{10}$(abundance + 1), and $\log_{10}$(biomass + 1). We, as others (Gray et al. 1998; Sheridan and Minello 2003), used an α = 0.01 significance level to reduce the risk of Type I errors, because the parametric assumptions were not always met for all our sampling periods and measures at α = 0.05 (Underwood 1981). Our statistical inferences, however, were robust as they were almost always the same at α = 0.01 and 0.05 in both standard two-way ANOVAs and in randomization tests for two-way ANOVAs with unequal variances (Manly and Francis 1999). Main factor (*habitat* and *year*) H_0 stated that there would be no significant differences in arithmetic (species richness) or geometric (abundance, biomass) means among habitats (i.e., no habitat variability) and years (i.e., no annual variability). The working H_0 for the presence/absence of recurring patterns stated that there would be no *habitat* × *year* interaction. Failing to reject a *habitat* × *year* interaction H_0 implies that the across-habitat pattern recurred annually on a ratio measurement scale (Sokal and Rohlf 1995). Two-way ANOVAs with a significant *habitat* effect were followed by one-way (*habitat*) ANOVAs and Tukey's multiple comparisons tests (Sokal and Rohlf 1995) to determine which habitat means were significantly different in each sampling period.

Natural seasonal and annual variability in the nekton community throughout Yaquina Bay (Bayer 1981; De Ben et al. 1990) confound the detection of recurring nekton–habitat patterns. To remove seasonal effects, we compared the nekton's habitat usage patterns in each sampling period over multiple years. To correct for potential annual variability, we compared the nekton's habitat usage patterns in relative terms. Relative means for each of our 10 measures of nekton community structure for each habitat were obtained by dividing their mean by the mean for *Zostera* habitat. We chose *Zostera* habitat as the standard because it was sampled in every sampling period and mean total nekton species richness, abundance, and biomass was always highest in it. *Zos-*

tera-habitat-standardized values — 1 for *Zostera* and decimal fractions for the other habitats — were converted to their equivalent relative integer values to make the across-habitat patterns more easily interpretable. For the *Zostera* habitat, the relative integer value was calculated as the reciprocal of the lowest relative decimal value. For the other habitats, it was the nekton measure relative decimal value multiplied by the relative integer value for *Zostera* habitat. For example, *Zostera*-habitat-standardized values of 1.0 (*Zostera*), 0.50 (*Upogebia*), 0.25 (*Neotrypaea*), and 0.05 (sand), for total nekton abundance in a sampling period would be converted to 20 (*Zostera*), 10 (*Upogebia*), 5 (*Neotrypaea*), and 1 (sand), since the reciprocal of the lowest *Zostera*-habitat-standardized decimal value is 1/0.05 = 20 = the relative integer value for the *Zostera* habitat, and other habitats' relative integer values are their relative decimal values (0.50, 0.25, and 0.05) × 20. Relative integer values for each nekton measure and habitat were averaged over all the sampling periods to obtain relative nekton habitat usage patterns for June through November.

Tests of binomial proportions (Rohlf and Sokal 1995) were conducted to determine whether the order of the habitat pair-wise rankings on each of our 10 measures of nekton community structure was random. The H_0 stated that there would be a binomial proportion = 0.5 (e.g., the frequency of *Zostera* > *Upogebia* = the frequency of *Zostera* < *Upogebia*; $\alpha = 0.05$) over the 10 (or 8 for comparisons with sand habitat) sampling periods.

Habitat pair-wise Z-tests (Zar 1984) were conducted to determine whether the percentages of samples collected with no nekton were significantly different ($\alpha = 0.05$).

We constructed an ecological periodic table with habitats as elements and total nekton Bray–Curtis similarity and mean total nekton species richness, abundance, and biomass as nekton properties. Global *R* and *R*-test results were used to infer the presence or absence and kind (habitat differences or no habitat differences) of periodic (year-over-year) patterns in total nekton Bray–Curtis similarity. Two-way ANOVA results were used to infer the presence or absence and kind of periodic patterns in mean total nekton species richness, abundance, and biomass. Non-significant *habitat* × *year* interactions meant a periodic pattern. Significant *habitat* × *year* interactions meant no periodic pattern. Significant *habitat* effects meant habitat differences. Non-significant *habitat* effects meant no habitat differences. The statistical inferences (data analyses in parentheses) used to organize the habitat elements in table were (A) habitat group rankings on mean total nekton species richness, abundance, and biomass (one-way ANOVAs and Tukey's multiple comparisons tests) and the temporal consistency of the rankings (tests of binomial proportions), and (B) habitat group rankings on the probability of collecting no nekton (*Z* tests). Relative mean values for total nekton species richness, abundance, and biomass during June through November for each habitat were included in the table.

Results

We collected a total of 454 nekton samples. On average, 11 (range 5–21) nekton samples were collected per habitat and sampling period. The mean (±SE) water depth at the time of sampling was 85 (±1.3) cm. Habitat-specific ranges in water temperature, salinity, and depth at the time of sampling, and *Zostera* percentage cover, *Upogebia* and *Neotrypaea* burrow hole density, and sediment %silt + clay at the beginning and end of our study (Table 1) are boundary conditions for those environmental variables beyond which the results of our study should not be extrapolated.

A total of 10 523 nekton specimens were collected, belonging to 64 taxa including 17 fish species, 10 crab, and 8 shrimp species. Over the entire study, saddleback gunnel (*Pholis ornata*, TL: 24.1–128.6 mm) was the dominant fish species, young-of-the-year Dungeness crab (*Cancer magister* CW: 3.2–37.4 mm) was the dominant crab, and Sitka coastal shrimp (*Heptacarpus sitchensis*) was the dominant shrimp.

Total nekton Bray–Curtis similarity was significantly different among habitats in every sampling period (global $R = 0.396–0.665$, $p < 0.001$) and in all habitat pair-wise comparisons ($R = 0.116–0.772$, $p < 0.05$; Table 2). MDS plots (Fig. 2) show the results graphically. These results indicate annually recurring across-habitat patterns of nominal differences in total nekton species composition and abundance.

Results of the one-way and two-way ANOVA and Tukey's multiple comparisons tests are presented and shown graphically for total nekton species richness, abundance, and biomass (Fig. 3). *Habitat* was significant in all the one- and two-way ANOVAs, indicating habitat differences in all the sampling periods. *Year* was significant in 9 of the 40 two-way ANOVAs, indicating annual variability in the means of total nekton species richness in sampling period 1 (Fig. 3), total nekton abundance in sampling period 2 (Fig. 3), crab species richness in sampling periods 1 and 4, crab abundance in sampling periods 1 and 4, crab biomass in sampling period 4, and shrimp abundance in sampling periods 1 and 4. *Habitat* × *year* interactions were always not significant. Significant *habitat* effects together with non-significant *habitat* × *year* interactions indicate annually recurring patterns of habitat differences for all 10 measures of nekton community structure.

Mean total nekton species richness and abundance always ranked as *Zostera* habitat > *Upogebia* habitat (10 of 10 sampling periods; $p < 0.05$), *Upogebia* habitat > *Neotrypaea* habitat (10 of 10 sampling periods; $p < 0.05$), and *Neotrypaea* habitat > sand habitat (8 of 8 sampling periods; $p < 0.05$) (Fig. 3). The same results, with one exception (*Upogebia* > *Neotrypaea* habitat in 8 of the 10 sampling periods [$p > 0.05$]), were obtained for mean total nekton biomass (Fig. 3).

Seventy percent (21 of 30) of the *Zostera* habitat versus *Upogebia* habitat, 97% (29 of 30) of the *Zostera* habitat versus *Neotrypaea* habitat, and 100% (24 of 24) of the *Zostera* habitat versus sand habitat comparisons on mean total nekton species richness, abundance, and biomass were statistically significant (Fig. 3). Fifteen percent (12 of 78) of the habitat pair-wise comparisons of mean total nekton species richness, abundance, and biomass were statistically significant between *Upogebia*, *Neotrypaea*, and sand habitats (Fig. 3).

Across-habitat rankings on fish and crab mean species richness, abundance, and biomass, and shrimp mean abundance were similar to those for total nekton, except the order *Upogebia* > *Neotrypaea* habitat was sometimes

Table 1. Ranges in percentage cover of *Zostera*, number of *Upogebia* and *Neotrypaea* burrow holes, and sediment %silt+clay at our sampling stations in 1998 and 2000, and water temperature, salinity, and depth, at the time of sampling by habitat and year.

Year	Cover (%)	Burrow holes (No. per 0.25 m^2)	Sediment (%silt+clay)	Temperature (°C)	Salinity (‰)	Depth (cm)
***Zostera* habitat**						
1998	35–100	—	3.8–51	9–18.5	30–36	25–125
1999	—	—	—	10.5–19.1	21–36	57–143
2000	15–100	—	2.1–46	11.9–18.2	24–36	35–145
***Upogebia* habitat**						
1998	—	17–285	12–53	12–19.5	31–36	35–135
1999	—	—	—	10.6–20.5	23–36	50–148
2000	—	1–112	3–51	11.4–18.6	21–36	41–135
***Neotrypaea* habitat**						
1998	—	12–554	4.7–48	12–23	31–35	40–140
1999	—	—	—	10.5–21.7	10–36	25–140
2000	—	17–244	0.6–23	11.2–19.9	21–36	18–124
Sand habitat						
1998	—	—	2.8–6.8	—	—	—
1999	—	—	—	9.4–16.9	26–36	48–145
2000	—	—	0.7–24	10.3–16.7	29–36	33–125

Note: —, no data or not applicable.

Table 2. The *R* statistic and significance level (*p*) of habitat pairwise comparisons of total nekton Bray–Curtis similarity for years 1998, 1999, and 2000.

Habitats	*R*	*p*
1998		
Neotrypaea vs. *Upogebia*	0.116	0.04
Neotrypaea vs. *Zostera*	0.689	0.001
Upogebia vs. *Zostera*	0.349	0.001
1999		
Sand vs. *Neotrypaea*	0.248	0.002
Sand vs. *Upogebia*	0.185	0.001
Sand vs. *Zostera*	0.653	0.001
Neotrypaea vs. *Upogebia*	0.134	0.001
Neotrypaea vs. *Zostera*	0.684	0.001
Upogebia vs. *Zostera*	0.363	0.001
2000		
Sand vs. *Neotrypaea*	0.390	0.001
Sand vs. *Upogebia*	0.243	0.001
Sand vs. *Zostera*	0.727	0.001
Neotrypaea vs. *Upogebia*	0.333	0.001
Neotrypaea vs. *Zostera*	0.772	0.001
Upogebia vs. *Zostera*	0.282	0.001

reversed. Deviations from the typical pattern occurred most frequently for shrimp mean abundance, where the order was *Neotrypaea* > *Upogebia* habitat in 7 of the 10 sampling periods ($p > 0.05$).

Zostera-habitat-standardized values for each of our 10 measures of nekton community structure, averaged over the 10 sampling periods of our study, summarize our findings on relative nekton habitat usage patterns for June through November (Table 3).

Two of the 131 (2%) samples collected in the *Zostera* habitat, 11 of the 123 (9%) samples collected in the *Upogebia* habitat, 19 of the 123 (15%) samples collected in the *Neotrypaea* habitat, and 38 of the 77 (49%) samples collected in the sand habitat contained no nekton. Except for *Upogebia* and *Neotrypaea* habitat, the differences in percentages are significant (*Z* test, $p < 0.05$).

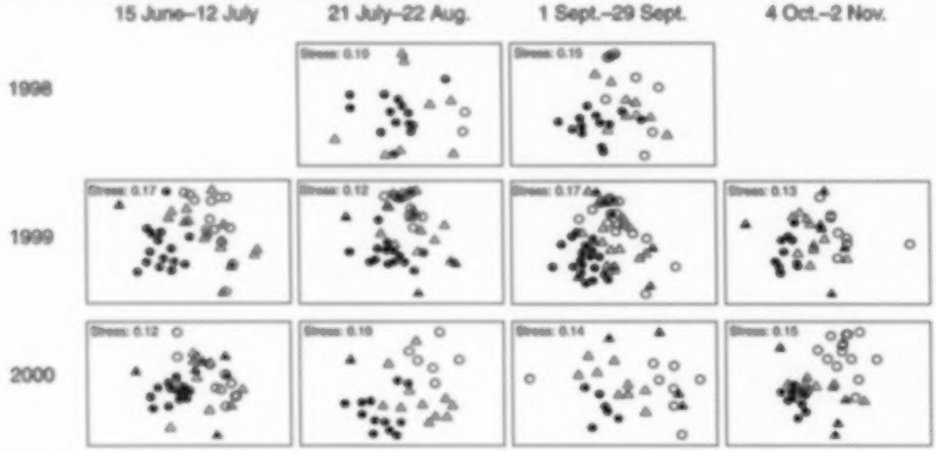
Ecological periodic tables

We systematically (Fig. 4) organized our findings on periodic (year-over-year) across-habitat patterns by the total nekton community in an ecological periodic table (Fig. 5). A habitat's entry in the table was predicated on the occurrence of periodic patterns in total nekton Bray–Curtis similarity (Table 2; Fig. 2). No periodic patterns would have indicated a flaw in our operational definition of habitat or nekton community (Jax 2006). The latter was unlikely, since we followed sound scientific principles in our field sampling methods and design (Green 1979; Krebs 1989; Rozas and Minello 1997). Periodic patterns in total nekton Bray–Curtis similarity may be either of habitat differences or no habitat differences. When there are periodic patterns of no habitat differences, the habitats are isotopes (from the Greek *iso* (same) and *topos* (place)) in the sense that they should occupy the same place in the table, since their nekton communities are consistently indistinguishable. Since there were always periodic patterns of habitat differences in total nekton Bray–Curtis similarity (Table 2; Fig. 2), there are no habitat isotopes in our ecological periodic table.

The rows in our table reflect the habitats' rank order on (A) mean total nekton species richness, abundance, and biomass (row 1, high; row 2, intermediate; and row 3, low) (Fig. 3), and (B) probabilities of occupation by nekton (row 1, low (~2%); row 2, intermediate (9–15%); and row 3, high (~49%) probability of no nekton in a 1.8 m^2 sample). When, as in this case, the habitats' rank order on (A) and (B) are complementary, the rows convey rank order information on both (A) and (B). When they are not complementary, two separate tables would have to be constructed.

The absence of *habitat* × *year* interactions (Fig. 3)

Fig. 2. Non-metric multidimensional scaling (MDS) plots of total nekton Bray–Curtis similarity in Yaquina Bay in 1998 (21 July – 22 August, 1–29 September); 1999 and 2000 (15 June – 12 July, 21 July – 22 August, 1–29 September, 4 October – 2 November). All analyses were conducted on raw, square-root-transformed data. Filled circles (●), *Zostera*; open triangles (△), *Upogebia*; open circles (○), *Neotrypaea*; filled triangles (▲), sand. Bray–Curtis similarity for total nekton was significantly different among habitats in every sampling period (global $R = 0.396–0.665$, $p < 0.001$) and in all habitat pair-wise comparisons.



means that the across-habitat patterns on relative mean total nekton species richness, abundance, and biomass were statistically indistinguishable year-over-year. For finer temporal (ca. monthly) scale reporting of relative habitat usage patterns, we could have constructed separate tables for each of our four sampling periods and entered them in a four-layered ecological periodic table. However, for simplicity and greater general utility, we time-averaged the relative mean values for each of the total nekton measures in all the sampling periods (Table 3) and entered them in a single ecological periodic table for June–November (Fig. 5). In summary, our ecological periodic table reports that at high tides from June to November in Yaquina Bay total nekton species richness, abundance, and biomass are, respectively, on average, 8 ×, 25 ×, and 25× greater in the *Zostera* habitat, 4 ×, 6 ×, and 5× greater in the *Upogebia* habitat, and 2 ×, 3 ×, and 2× greater in the *Neotrypaea* habitat than in sand habitat. Similar ecological periodic tables could be constructed for fish, crab, and shrimp communities using the information in Table 3.

Discussion

The nekton–habitat patterns we found validate the ecological relevance of our habitat types to nekton. The evidence includes annually recurring across-habitat patterns in total nekton species composition and abundance and 10 measures of nekton community structure that are also indicators of habitat quality and preference (Rozas and Minello 1998) and are partial indicators of the value of these habitats as nurseries for nekton (Beck et al. 2001; Heck et al. 2003). The differences in the habitat means of our 10 nekton measures varied by factors (2–25×) that most experts would deem ecologically significant. Differences in the frequency with which nekton was absent from the samples collected within each habitat (2% in the *Zostera* habitat, 9%–15% in the *Upogebia* and *Neotrypaea* habitats, and 49% in sand) also indicate marked differences in habitat usage by nekton.

We are unaware of any previous studies of nekton in *Upogebia* or *Neotrypaea* habitats. Other investigators, however, may not have distinguished them from unvegetated mudflats. The results of other studies of nekton in US Pacific Northwest estuaries (e.g., Bayer 1981; Murphy et al. 2000; Johnson and Thedinga 2005) are consistent with the general observation that nekton species richness and abundance tends to be higher in vegetated than unvegetated habitat (Hemminga and Duarte 2000; Jackson et al. 2001). Their sampling methods and designs, however, preclude reliable inferences about recurring quantitative across-habitat patterns. For example, they sampled at only one or a few nonrandom stations in each habitat, so their results may not be broadly representative (Green 1979). And their use of sampling gear (e.g., beach seines, trawls, fyke nets) with different nekton catch efficiencies in different habitats (Rozas and Minello 1997) confounded habitat and sample gear effects. Another common shortcoming was their failure to sample at comparable times in the nekton's natural temporal (tidal, diel, monthly, or seasonal) cycles, thus confounding the natural cyclical variability in nekton abundance with the association of nekton with habitats (Jackson et al. 2001).

Few studies have identified recurring quantitative animal–habitat patterns in estuaries (Boström et al. 2006; Connolly and Hindell 2006). Mitchell (2005, p. 634) attributes this to an inherent inability to operationally define habitats in an ecologically meaningful way. His thesis is that "our present concept(s) of habitat are of value only as qualitative descriptors of organism distribution, and are of little value in quantitatively describing organism abundance. As such, the concepts are of very limited use in basic or applied ecology, or quantitative management of populations." We think that discovering habitat character sets that are quantitatively predictive of animal distributions is challenging, but not impossible, and that the primary impediment to discovering them has been the use of flawed operational definitions of the population or community of interest due to the use of inap-

Fig. 3. Bar plots of mean total nekton species richness, abundance, and biomass in four intertidal habitats (*Zostera marina* (Zm), *Upogebia pugettensis* (*Up*), *Neotrypaea californiensis* (*Nc*), and Sand; sampled by cylindrical drop sampler, surface area 1.8 m^2) in Yaquina Bay during four sampling periods (15 June – 12 July; 21 July – 22 August; 1–29 September; and 4 October – 2 November) in 1998 (striped bars), 1999 (gray bars), and 2000 (black bars). White bars indicate no data. Significant ($p < 0.01$) habitat, year, and habitat × year effects in two-way analyses of variance (ANOVAs) are indicated by an asterisk (*). Bars with the same letters above them mark mean indicator values that were not significantly different during the year and sampling period indicated.

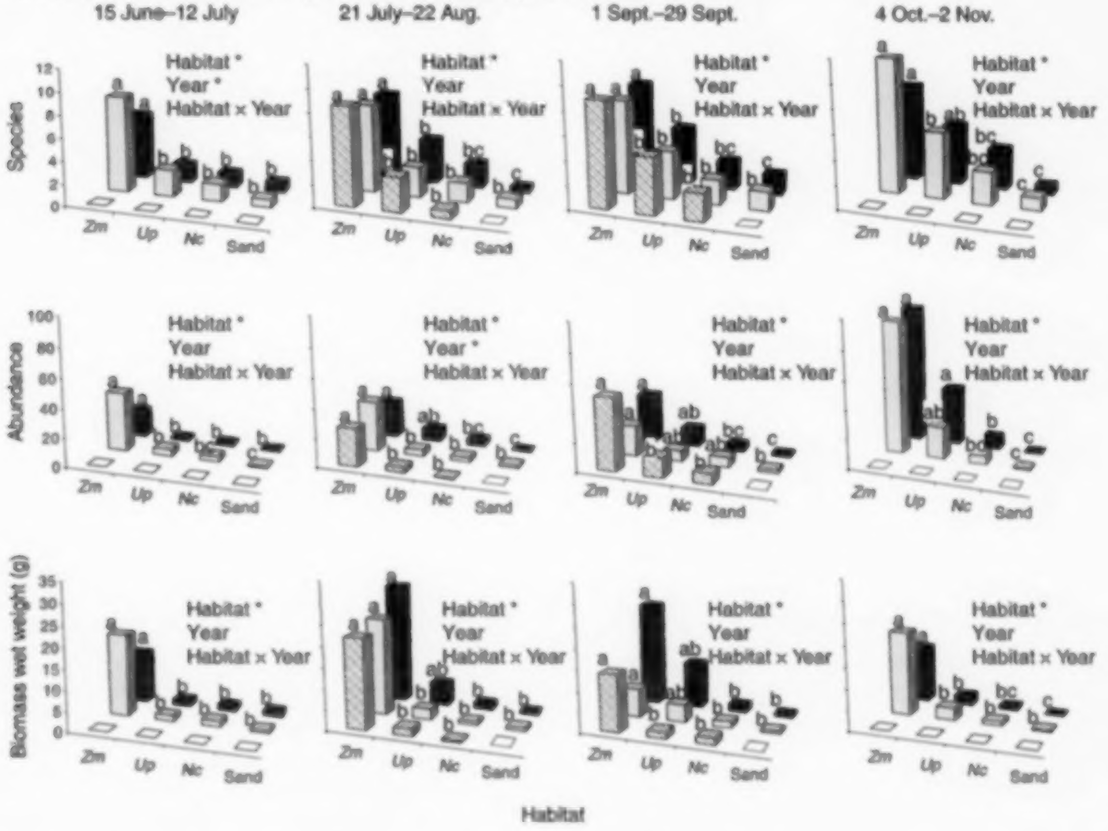


Table 3. Time-averaged (June to November), standardized values of 10 measures of nekton community structure.

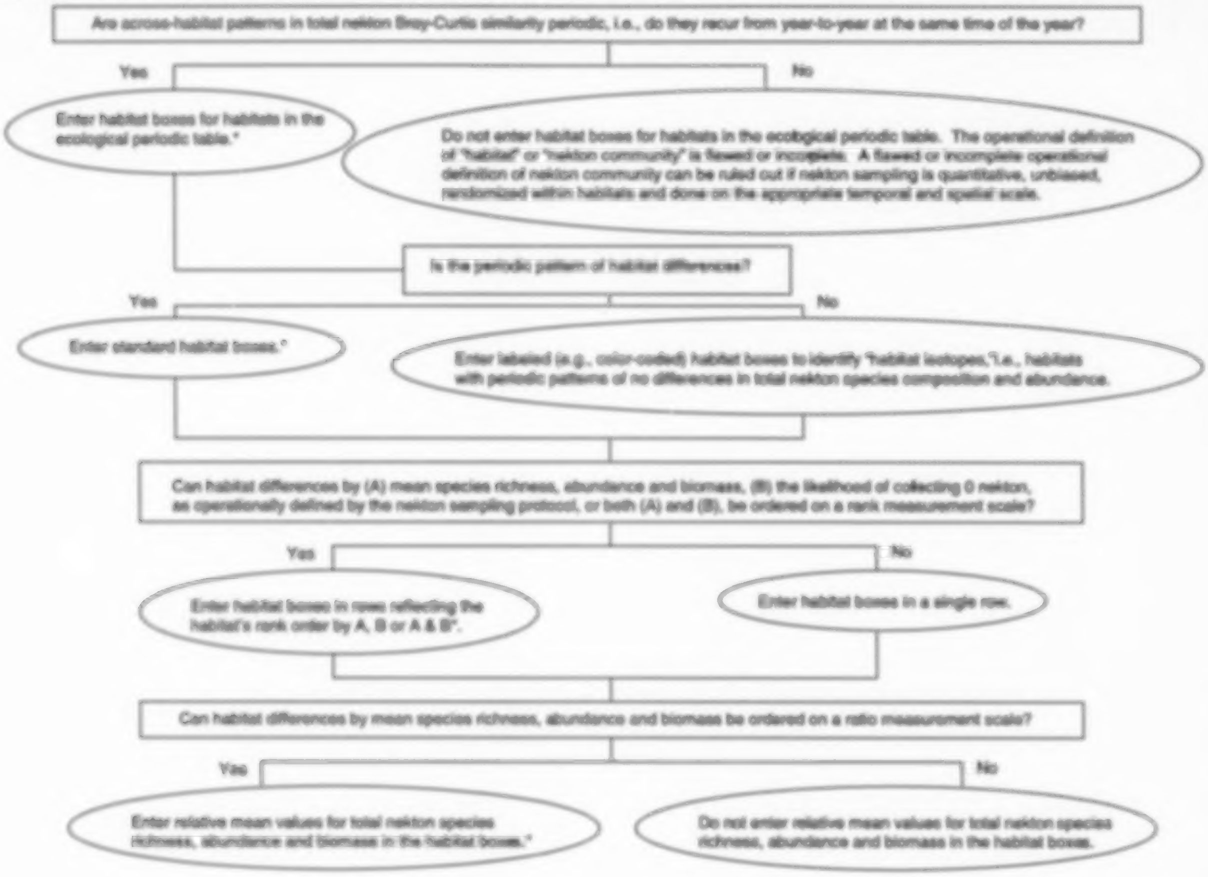
Nekton measure	Habitat *Zostera*	 *Upogebia*	 *Neotrypaea*
Total nekton species richness	8	4	2
Total nekton abundance	25	6	3
Total nekton biomass	25	5	2
Fish species richness	8	3	2
Fish abundance	20	3	6
Fish biomass	20	3	2
Crab species richness	8	4	2
Crab abundance	20	7	2
Crab biomass	20	11	2
Shrimp abundance	20	4	6

Note: Sand habitat = 1 for all nekton measures.

propriate sampling methods or study designs (Boström et al. 2006; Connolly and Hindell 2006). Without this impediment, quantitative animal–habitat patterns have been found for coral-reef-dwelling fish (Holbrook et al. 2000; Wellenreuther et al. 2008), freshwater benthic macrofauna (Rabeni et al. 2002), estuarine benthic macrofauna (Ferraro and Cole 2007), and nekton (this study).

The periodic nekton–habitat patterns we found and used to construct an ecological periodic table are, in Dodds' (2009, p. 70) framework, "strong patterns" as they are "empirical observations with mechanisms not well enough established or too limited by constraints to be considered laws." In Pickett et al.'s (1994) terminology, they are "probabilistic laws." All natural patterns have constraints and exceptions (Dodds 2009). The spatial constraint on our periodic nekton–habitat patterns is Yaquina Bay. Several environmental constraints are given in Table 1. Temporal constraints are fixed by the time frame (daytime high tides, June–November) of our study. Our drop sampler provided unbiased, quantitative sampling in all the habitats (Rozas and Minello 1997). But its small size (1.8 m^2) made statistical comparisons between habitats with low nekton densities difficult. Whether or not the patterns we found hold up over broader spatial and temporal scales and over a wider range of environmental conditions, are subjects for further study. Since

Fig. 4. Decision tree for constructing an ecological periodic table for total nekton habitat usage. The decisions in the construction of Fig. 5 are marked with an asterisk (*).

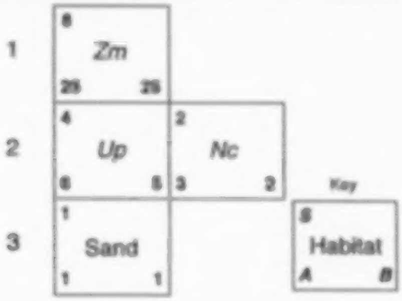

Are across-habitat patterns in total nekton Bray-Curtis similarity periodic, i.e., do they recur from year-to-year at the same time of the year?
Yes
No
Enter habitat boxes for habitats in the ecological periodic table.*
Do not enter habitat boxes for habitats in the ecological periodic table. The operational definition of "habitat" or "nekton community" is flawed or incomplete. A flawed or incomplete operational definition of nekton community can be ruled out if nekton sampling is quantitative, unbiased, randomized within habitats and done on the appropriate temporal and spatial scale.
Is the periodic pattern of habitat differences?
Yes
No
Enter standard habitat boxes.*
Enter labeled (e.g., color-coded) habitat boxes to identify "habitat isotopes,"i.e., habitats with periodic patterns of no differences in total nekton species composition and abundance.
Can habitat differences by (A) mean species richness, abundance and biomass, (B) the likelihood of collecting 0 nekton, as operationally defined by the nekton sampling protocol, or both (A) and (B), be ordered on a rank measurement scale?
Yes
No
Enter habitat boxes in rows reflecting the habitat's rank order by A, B or A & B*.
Enter habitat boxes in a single row.
Can habitat differences by mean species richness, abundance and biomass be ordered on a ratio measurement scale?
Yes
No
Enter relative mean values for total nekton species richness, abundance and biomass in the habitat boxes.*
Do not enter relative mean values for total nekton species richness, abundance and biomass in the habitat boxes.

many other US Pacific Northwest estuaries are hydrologically and geomorphologically similar to Yaquina Bay (Lee et al. 2007), we predict that at least some of the patterns will be more widely applicable. Biogeographic ranges of the populations or communities of interest will, obviously, set spatial limits on their animal–habitat patterns. Even so, there may be some commonalities in community-level habitat patterns across biogeographical regions.

The value of knowing natural patterns is determined by how useful they are (Dodds 2009). We predict ecological periodic tables will be highly valued for their multifunctionality just as the chemical periodic table is highly valued for its multifunctionality. Some anticipated uses of ecological periodic tables include validating habitat classification schemes (Allee et al. 2000), producing animal–habitat valuation maps needed to develop management strategies for the sustainable use and conservation of aquatic ecosystems (Derous et al. 2007), predicting the effects of habitat alterations on natural resources (Rönnbäck et al. 2007), providing habitat values in ecological risk models (Obery and Landis 2002), aiding in the site location and managing of estuarine and marine reserves (Ward et al. 1999; Lindsay et al. 2008), setting success criteria for restoration projects (Short et al. 2000), and setting appropriate remediation guidelines in habitat equivalency and compensatory restoration analyses (Kennish 2000; Fonseca et al. 2002). Their most important scientific use may be in providing a basis for and context to properly design studies capable of identifying the processes that are the underlying causes for natural patterns (Underwood et al. 2000).

Southwood (1977) used the phrase "a sort of ecological periodic table" because organisms evolve and they may directly influence their habitat. Consequently, unlike chemical elements, the elements in ecological periodic tables (habitats) can change. Also, unlike chemical elements which are "natural kinds" (Scerri 2007), habitats are human constructs that, if they are to be predictive of animal distributions, must include habitat characters that are necessary and sufficient for that purpose (Andrewartha and Birch 1954; Southwood 1977; Jax 2006). Ecological periodic tables serve as repositories of and sources for that predictive information. How and why we defined habitats as we did is explained in the Introduction. Had there not been periodic across-habitat patterns for one or more of our habitat types, their operational definitions would have been deemed flawed or incomplete (Jax 2006).

Fig. 5. An ecological periodic table for total nekton usage of four intertidal habitats in Yaquina Bay during high tides from June through November. Boxes represent habitat types: *Zm*, *Zostera marina*; *Up*, *Upogebia pugettensis*; *Nc*, *Neotrypaea californiensis*; and Sand, sand. A habitat's entry in the table signifies there were periodically recurring (year-over-year) across-habitat patterns of nominal differences in total nekton species composition and abundance. Rows in the table classify the habitats by their typical rank order on both (A) mean total nekton species richness, abundance, and biomass (row 1, highest; row 2, intermediate, and row 3, lowest) and (B) probabilities of occupation by nekton (row 1, low (~2%); row 2, intermediate (9–15%); and row 3, high (~49%) probability of no nekton in a 1.8 m^2 sample). The numbers in the corners of each habitat box are relative mean values for total nekton species richness (*S*), abundance (*A*), and biomass (*B*).



The nekton properties in our ecological periodic table are commonly used measures of community composition and structure. Measurements of animal population and community properties will vary depending upon the sampling protocol used. Ecologists, in general, have been slow to seek out and adopt cost-efficient, standardized field sampling methods and designs, prompting Krebs (1989, p. 197) to remark "There is probably more money wasted in ecological research by the use of poorly designed studies than anyone cares to guess." To minimize waste, unnecessary multiple versions of and the need to frequently revise ecological periodic tables, researchers need to identify efficient, quantitative sampling methods and designs capable of distinguishing ecologically important differences between the habitat types of interest and to standardize their use.

There were >700 different versions of the chemical periodic table during its development and even today chemists do not agree on its best configuration (Scerri 2007). We would expect ecologists to be no less opinionated about the best version and configuration of ecological periodic tables. We don't claim that our version is the best. On this matter we encourage open-mindedness and suggest that Darwinian selection be allowed to determine the winners.

Ecological periodic tables, we believe, could be as iconic as chemical periodic tables. There are probably many uses of ecological periodic tables (e.g., pedagogical) that we cannot anticipate. We have no doubt that obtaining and systematically organizing information about predictive natural patterns will serve science well and benefit its practitioners.

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Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management

Isaac C. Kaplan, Phillip S. Levin, Merrick Burden, and Elizabeth A. Fulton

Abstract: Any fishery management scheme, such as individual fishing quotas (IFQs) or marine protected areas, should be designed to be robust to potential shifts in the biophysical system. Here we couple possible catch scenarios under an IFQ scheme with ocean acidification impacts on shelled benthos and plankton, using an Atlantis ecosystem model for the US West Coast. IFQ harvest scenarios alone, in most cases, did not have strong impacts on the food web, beyond the direct effects on harvested species. However, when we added the impacts of ocean acidification, the abundance of commercially important groundfish such as English sole (*Pleuronectes vetulus*), arrowtooth flounder (*Atheresthes stomias*), and yellowtail rockfish (*Sebastes flavidus*) declined up to 20%–80%, owing to the loss of shelled prey items from their diet. English sole exhibited a 10-fold decline in potential catch and economic yield when confronted with strong acidification impacts on shelled benthos. Therefore, it seems prudent to complement IFQs with careful consideration of potential global change effects such as acidification. Our analysis provides an example of how new ecosystem modeling tools that evaluate cumulative impacts can be integrated with established management reference points and decision mechanisms.

Résumé : Tous les schémas d'aménagement de la pêche, tels que les quotas individuels de pêche (IFQ) et les zones de protection marine, devraient être planifiés de manière à demeurer robustes face à des variations potentielles dans le système biophysique. Nous associons ici des scénarios de capture possibles dans un projet d'IFQ à des impacts de l'acidification de l'océan sur le benthos à coquilles et le plancton, à l'aide d'un modèle d'écosystème Atlantis pour la côte ouest des É.-U. Dans la plupart des cas, les scénarios de récolte IFQ par eux-mêmes n'ont pas d'impact important sur le réseau alimentaire, au-delà des effets directs sur les espèces récoltées. Cependant, lorsqu'on ajoute les impacts de l'acidification de l'océan, l'abondance de poissons de fond d'importance commerciale, tels que la sole anglaise (*Pleuronectes vetulus*), la plie à grande bouche (*Atherestes stomias*) et le sébaste à queue jaune (*Sebastes flavidus*), décroît de jusqu'à 20–80 % à cause de la perte des proies à coquilles dans leur régime alimentaire. La sole anglaise connaît une réduction de dix fois dans la capture potentielle et le rendement économique en présence de forts impacts de l'acidification sur le benthos à coquilles. C'est pourquoi, il paraît prudent améliorer les IFQ en portant une attention particulière aux effets potentiels du changement climatique, tels que l'acidification. Notre analyse est un exemple illustrant comment les nouveaux outils de modélisation des écosystèmes qui évaluent les impacts cumulatifs peuvent être intégrés aux points de référence de gestion établis et aux mécanismes décisionnels.

[Traduit par la Rédaction]

Introduction

The social, economic, and political context for fisheries management and conservation is daunting, involving overcapacity of fishing fleets, perverse economic incentives, lack of international governance, and rising seafood demand (Hilborn et al. 2004; Pauly et al. 2005; Branch et al. 2006*a*). In many ways, these problems have been more vexing than the complicated underlying biological processes such as recruitment (i.e., the production of juveniles), dispersal of larvae, and annual or decadal shifts in ocean condition (Chavez et al. 1999; Hare and Mantua 2000; Kinlan and Gaines 2003). Fishery management tools that seek to address these problems include marine protected areas (Halpern and Warner 2002), payments to fishers in exchange for exiting the fishery (Holland et al. 1999), international fishery treaties (Levesque 2008), and seafood eco-labeling (Potts and Haward 2007), in addition to more traditional approaches such as caps on catch, landings, and effort. Catch shares, or individual fishing quotas (IFQs), have been implemented in

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some jurisdictions as a promising method to address many of the core problems related to fisher behavior, incentives, and governance (US Commission on Ocean Policy 2004; Costello et al. 2008; Heal and Schlenker 2008). IFQs allocate individual fishers a set portion or share of the total catch. Frequently these catch shares can be traded between vessels, similar to cap and trade systems for atmospheric pollution. Increased flexibility and certainty under catch shares should improve profitability and reduce overcapitalization (Branch et al. 2006*a*). A guaranteed long-term stake in the resource can also align fisher incentives towards more sustainable fishing practices and conservation-oriented management decision, such as lower quotas (Branch 2009).

While catch share schemes show promise as management tools, they still must effectively account for the realities of the biophysical system. Cumulative impacts such as climate change, ocean acidification, and habitat degradation threaten the productivity of marine systems beyond the fishing impacts mitigated by catch shares. Climate change and ocean acidification are separate but related phenomena, both driven by anthropogenic release of CO_2, and are among the most pressing concerns. Scenarios for fossil fuel emissions suggest an increase in CO_2 levels from the current 385 ppmv (718 mg/m^3 at 14.5 °C) to at least 750 ppmv (1398 mg/m^3 at 14.5 °C) (IPCC 2001) and possibly higher than 1000 ppmv (1865 mg/m^3 at 14.5 °C) by the year 2100 (Royal Society 2005). In the oceans this is likely to lead to 1.8–4 °C increases in sea surface temperature and declines in pH of 0.14–0.35 (IPCC 2007) or as extreme as 0.3–0.5 (Caldeira and Wickett 2005), from a current level of ~ pH 8.1. Reductions in pH of this magnitude could lead to mortality of shell-forming corals, benthos, and plankton groups, owing to reduced calcification rates in an acidic ocean (Fabry et al. 2008; Hall-Spencer et al. 2008). Shifts in temperature and subsequent alterations to climate may lead to shifts in the distribution and foraging of vertebrates and reduced reproductive success (Bograd et al. 2009). Thus we suggest that any fisheries policy, including IFQs, should be considered in light of scenarios for global change. In a departure from what is familiar to fisheries managers, the biological implications of ocean acidification or rising temperatures could in the future become more important than social and economic effects.

Here we present a case study of the US West Coast, where the Pacific Fishery Management Council recently began the implementation of an IFQ program for the groundfish trawl fleet. For this particular fishery, a combination of IFQs and expansion of on-board observer coverage is expected to increase individual accountability and to reduce bycatch and discard rates, but IFQs will not radically change the fishing mortality rates on most target species. Beginning in 1983, the Fishery Management Council imposed increasingly strict per-vessel landings limits, and in 1994 the Council dramatically reduced open-access entry to the fishery. In 2000, the Secretary of Commerce declared the West Coast a federal fishery disaster, and since then, mandatory rebuilding plans have severely limited catches on over nine species (Field 2004). Thus, compared with cases where IFQs are imposed on previously unregulated fisheries, we expect the impacts of IFQs on West Coast groundfish to be more subtle, and more focused on bycatch species or previously lightly-exploited target species.

This US West Coast trawl fishery primarily targets benthic species that derive a substantial portion of their diet from shelled organisms, which may show the greatest declines under future ocean acidification. The fleet targets species such as Dover sole (*Microstomus pacificus*), English sole (*Pleuronectes vetulus*), sablefish (*Anopoploma fimbria*), rockfish (*Sebastes* spp.), and thornyhead (*Sebastolobus* spp.). Shelled organisms such as bivalves, snails, sea urchins, sea stars, brittle stars, and euphausiids compose up to 35% of the diets of some flatfish and rockfish groups (Buckley et al. 1999). Loss of these diet items may cause declines in biomass and landings of target species, separate from what would be expected under simple assumptions about harvest under IFQs.

In this exploration, we couple possible catch scenarios under an IFQ fishery with ocean acidification impacts, using an Atlantis ecosystem model for the US West Coast (Brand et al. 2007; Kaplan and Levin 2009). The ecosystem model includes the full food web, oceanography, and fisheries. Our intent is to evaluate the impact of IFQs and acidification on the ecosystem, but also to illustrate an overall approach that links tools like Atlantis to the established system of single-species reference points that underlie current management and conservation decisions. Specifically, we evaluate (*i*) the direct effects of fishing under IFQs, (*ii*) whether the performance of IFQ scenarios varies in the face of ocean acidification and subsequent declines in benthic and planktonic prey species, and (*iii*) the indirect effects, primarily through predator–prey linkages, that result from fishing under IFQs and from ocean acidification.

We present the results using biological reference points and decision tables (Hilborn and Walters 1992) that are familiar to fisheries managers, but which are informed by a full consideration of the cumulative impacts of fishing, trophic effects, and ocean acidification. Our analyses demonstrate the importance of building global change projections into natural resource management plans, and the pitfalls that face policy makers who focus only on the direct human impact (fishing) rather than cumulative anthropogenic impacts.

Materials and methods

Harvest scenarios and rationale

We developed four scenarios for future catch (landings + discards) that reflect likely fisher behavior under the new incentives and flexibility expected with IFQs for the US West Coast groundfish trawl fleet. The catch scenarios and the analyses supporting them (see supplementary data,[3] Appendix S1) derive from an accepted model used by fishery decision makers on the US West Coast (PFMC 2003). The scenarios reflect the possibility that the incentives created through IFQs may lead fishermen to improve their ability to avoid overfished rockfish species that have very low quotas, thereby allowing the vessels to catch higher amounts of target species. Overfished species include canary rockfish (*Sebastes pinniger*), yelloweye rockfish (*S. ruberrimus*), darkblotched rockfish (*S. crameri*), Pacific ocean perch (*S. alutus*), bocaccio rockfish (*S. paucispinis*), and cowcod (*S. levis*). Target species with the potential for higher catches include arrowtooth flounder (*Atheresthes stomias*), Dover sole (*Microstomus pacificus*), shortspine (*Sebastolobus alascanus*) and longspine thornyheads (*S. altivelis*), slope rockfish, chilipepper rockfish (*Sebastes goodei*), yellowtail rockfish (*S. flavidus*), lingcod (*Ophiodon elongatus*), and various flatfish species that make up the "other flatfish" complex.

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[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca)

We consider four catch scenarios. In the Status Quo scenario, catches per species and area occur based on the assumption that regulations in the future are the same as those set between 2003 and 2006. Catches of target and bycatch species under this scenario are roughly the same as those that occurred from 2003 to 2006. In Scenario 1 (Low Catch scenario), fishermen have only minimal success at avoiding overfished species, and therefore can only minimally increase catches of target species compared with the Status Quo scenario. Bycatch rates (kilograms overfished rockfish bycatch/kilograms target species) are assumed to be 55% of Status Quo. In Scenario 2 (Medium Catch scenario), fishermen have moderate success at avoiding catch of overfished species, and therefore can increase catch of some target species. Bycatch rates are assumed to be 30% of Status Quo. In Scenario 3 (High Catch scenario), fishermen are highly successful at avoiding overfished species, and therefore can substantially increase catch of target species. Bycatch rates are assumed to be 15% of Status Quo.

Note that in all scenarios, total catches of overfished species (e.g., canary rockfish) remain constant or increase slightly even though the bycatch rate may decline; the catch of target species is the main driver that we explore here. Catch of several flatfish species varies more than other stocks because their catches are currently well below allowable levels, and therefore can be harvested in much higher quantities than are harvested currently. Catches of many other stocks, such as sablefish and spiny dogfish (*Squalus acanthias*), are already near allowable levels specified by the Pacific Fishery Management Council, are constrained to a greater degree by encounters of overfished stocks, or have limited markets and are therefore not actively pursued.

We do not simulate the full management response to changes in fish abundance; instead we use simple constant catch scenarios. Simulating the full management response would involve modeling a harvest control rule, and the appropriate lags in implementation and monitoring. The Pacific Fishery Management Council's current threshold control rule specifies a fixed fishing mortality rate when biomass is above 40% of unfished levels, and proportional decreases in this rate as biomass falls from 40% to 10% of unfished levels (PFMC and NMFS 2009). Most species are assessed every 2–4 years, with lags of approximately one year for monitoring and policy implementation. Although we do not simulate the management process, Fulton et al. (2007) have used Atlantis to do so in Australia, and ultimately our approach here could be extended to include this in a management strategy evaluation framework (MSE; Sainsbury et al. 2000).

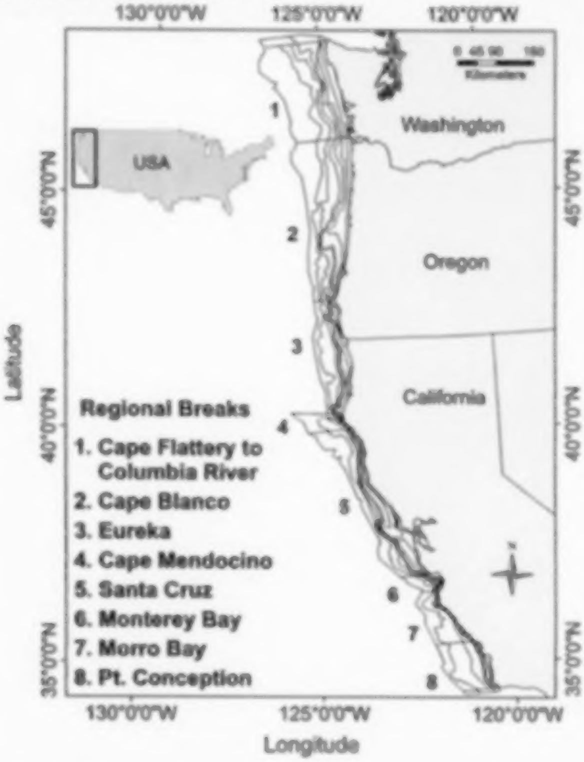
The Atlantis ecosystem model for the California Current

The Atlantis ecosystem model for the California Current (Brand et al. 2007; Kaplan and Levin 2009) is built to address the impacts of climate, oceanography, nutrient dynamics, and spatially explicit fishing effort on a dynamic food web. The generic Atlantis code is well developed at this time, and Fulton (2001; 2004) and Fulton et al. (2005; 2007) have parameterized it for several systems in Australia. Most recently, Fulton et al. (2007) have used the southeastern Australia model to rank alternative policy scenarios, quantitatively evaluating alternative management packages of quotas, protected areas, closed seasons, and other policy options.

Atlantis is a flexible modeling framework that includes many options for modeling ecology, oceanography, fisheries, and management. Key ecological options and assumptions in the present application and in most other Atlantis models built to date include density dependent movement, with predators moving toward areas with higher food availability; forced migrations into and out of the model domain (e.g., for highly migratory species such as whales); reproduction based on standard Beverton Holt stock recruitment relationships (for fish) and fixed offspring/adult (for mammals and birds); predation governed by a modified Holling Type II functional response with gape limitation, allowing predator diets to vary in relation to prey availability and prey length relative to the predator's length; and dynamic weight-at-age, meaning that realized consumption rates throughout the modeled time period translate into variable weight-at-age of each cohort. Primary production is influenced by temperature, light, and nutrient availability, with nutrients and plankton advected by current fields. Though many options for these ecological processes are available within the Atlantis code base, analyses by Fulton (2001; 2004) and Fulton et al. (2003; 2004) have supported the appropriateness of these particular representations, in particular for the functional response, physiological detail, and typical levels of aggregation for functional groups and spatial cells.

Our California Current Atlantis model extends from the US–Canada border to Point Conception, California, and out to the 1200 m isobath (Fig. 1). The trophic dynamics are represented by 55 functional groups in the food web (see supplementary data,[3] Appendix S2, Tables S2.1–S2.2). Functional groups are typically composed of pools of 1–10 species with similar ecological roles. General classes of functional groups include habitat-forming species like kelp, corals, and sponges, as well as vertebrate consumers, benthic invertebrates, zooplankton, phytoplankton, and detritus. Vertebrate populations have age structure, and Atlantis explicitly tracks weight-at-age. The model is divided into 62 spatial zones, each with up to seven depth layers. Although we do not address these questions here, the spatial structure of the model allows us to explicitly test hypotheses regarding fish migrations and movement behavior, fleet dynamics, and spatial management. The model is forced with daily hydrodynamic flows, salinity, and temperature outputs from a high-resolution three-dimensional Regional Ocean Modeling System (www.myroms.org), implemented by E. Curchitser and K. Hedstrom (Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Road, New Brunswick, New Jersey, USA, personal communication, 2009), and recently

Fig. 1. Spatial extent of the Atlantis ecosystem model for the California Current Atlantis. The region includes 62 spatial boxes ranging from the coastline to 2400 m.



applied by Hermann et al. (2009). A separate sub-module simulates simplified effort dynamics for fisheries. The full parameterization for the California Current is available in Brand et al. (2007).

Initial conditions for the model (e.g., biomass or numbers-at-age, and spatial distributions) represent approximately 1995–2005, and are taken from sources detailed in Brand et al. (2007). Briefly, for biological groups these sources include a 1998–2003 continental shelf and slope trawl survey for most fish species (e.g., Keller et al. 2006), published stock assessments for commercially harvested fish species, population assessments of mammals and birds, and in the absence of other information, mass-balance estimates of biomass (Field 2004). Initial nutrient and phytoplankton concentrations are taken primarily from 1997–2004 GLOBEC and 2000–2004 CALCOFI research cruises (Brand et al. 2007). Zooplankton initial abundance varies with depth and distance from shore, and was derived from a variety of research cruises from 1967–2003 off Newport and Brookings, Oregon. Benthic invertebrate abundances primarily derive from grab samples taken from 0–850 m off the coast of Washington and Oregon. Fish and mammal growth and consumption rates are dynamic, but under initial conditions these were set such that predicted growth rates (e.g., von Bertalanffy) matched observed growth rates reported in stock assessments. Stock–recruit parameters (and thus stock productivity) were informed by values in published stock assessments. These initial conditions defined model year 2009, the initiation of our simulations. The model has been calibrated in three phases: a first phase that tests the model's ability to reproduce unfished biomasses, which can be compared to estimates from stock assessments (Brand et al. 2007); a second phase that tests stock productivities under constant fishing rates, and a final phase that tests the model's ability to fit historical time series. A further description of the calibration methodology and the main parameters adjusted in each phase are found in Horne et al. (2010).

Modifications since the publication of Brand et al. (2007) primarily involve addition of canary rockfish and English sole groups (see supplementary data,[3] Appendix S2, Table S2.1), minor updates to stock abundance as reported in the 2007 stock assessments (PFMC 2008), and inclusion of updated diet data (Dufault et al. 2009). The new diet data are particularly important, since they dictate the links in the food web, and thus predator/prey interactions.

Incorporating catch scenarios and ocean acidification into the Atlantis ecosystem model

All model runs presented here begin with the same base parameterization and model behavior. The annual catch projections (see supplementary data,[3] Appendix S1, Table S1.1) were applied beginning in model year 2009, with these catches imposed for 20 years (through 2028).

We converted the catch scenarios (see supplementary data,[3] Appendix S1, Table S1.1) to annual catch estimates per functional group, and applied these catches beginning in model year 2009. This required matching regions defined in the catch projections with Atlantis regions (see supplementary data,[3] Appendix S3, Table S3.1), as well as matching the species from the catch projection to functional groups within Atlantis (online Supplemental Appendix S3, Table S3.2). For functional groups not listed in the catch scenarios (i.e., not contained in online Supplemental Appendix S1, Table S1.1[3]), we applied the final year of data we had from the PacFIN landings database (2004) to all projection years. These functional groups included five pelagic fish groups, four invertebrate groups, and only three demersal fish groups (skates and rays, shallow small rockfish, and deep miscellaneous fish). Annual catches were applied in each model year as long as they did not exceed the standing stock. We did not decrease harvests if biomass declined (i.e., we did not simulate a management response).

We represented ocean acidification as additional mortality on benthic shelled organisms, specifically the three benthic filter feeder groups (e.g., bivalves and corals), benthic herbivorous grazers (e.g., sea urchins), and deep macrozoobenthos (e.g., sea stars). We also considered possible effects on two plankton functional groups, large zooplankton (which include thecosome pteropods) and "small phytoplankton" (primary producers that are generally smaller than diatoms, including coccolithophores and foraminifera with photosynthetic endosymbionts) (see supplementary data,[3] Appendix S2, Table S2.2). Although in nature the effect of acidification likely differs between species within a functional group, here we simply model the aggregate effect on the total functional group.

Our simulations involving declines in benthos are informed by Hall-Spencer et al. (2008), who were the first to publish in-situ observations of declines in benthos under pH levels likely to occur in the next 100 years. Studying the area near underwater volcanic CO_2 vents, the authors found significantly depressed levels of limpets and near-zero abundance of sea urchins at sites with pH around 7.83. They also observed decreases in limpet and snail shell thickness with reduced pH. Laboratory studies on benthic invertebrates support these in situ observations (brittle stars: Dupont et al. 2008; sea urchins: Kurihara and Shirayama 2004; mussels and oysters: Gazeau et al. 2007; Kurihara et al. 2007; 2009). However, the laboratory studies frequently use unrealistically low pH levels, focus on juvenile stages only, and cannot usually be translated directly onto the population level. Many of these studies of benthic invertebrates (excluding corals) have been reviewed in Fabry et al. (2008). For corals, laboratory studies on a limited number of species suggest that acidification can cause declines in calcification of 4.5%–40% when standardized to a pCO_2 of ~420 ppmv (Kleypas and Langdon 2006, their Table 3). Guinotte et al. (2003) extended the modeling work of Kleypas et al. (1999) and predicted that even conservative projections of atmospheric CO_2 level rise by the year 2069 will reduce the whole Pacific Ocean to be marginal habitat for coral reefs.

Our simulations involving acidification impacts on plankton stem from laboratory experiments on large zooplankton (pteropods) and small phytoplankton (foraminifera and coccolithophores). Our modeling of large zooplankton response to acidification is informed by experiments with the pteropod *Clio pyramidata* that demonstrated shell dissolution within 48 h of being exposed to ocean chemistry similar to that predicted for 2100 (Feely et al. 2004; Orr et al. 2005; Fabry et al. 2008). The effects of acidification on coccolithophores have been demonstrated by Riebesell et al. (2000), who found 16%–45% decreases in calcification rates at CO_2 levels of 750 ppmv. Other authors have pointed out that the responses of coccolithophores may also be species specific (Langer et al. 2006), and there is evidence for slight increases in carbon fixation rates under higher CO_2 concentrations (Riebesell et al. 2000). Evidence for negative impacts of 4%–14% on foraminifera under pH expected in 2100 is summarized in Fabry et al. (2008), but laboratory experiments have only been conducted on two of ~54 species.

Owing to the lack of quantitative laboratory experiments that translate realistic future pH into mortality rates, we used the studies above primarily to point to the functional groups that are most likely to suffer under ocean acidification. There is a strong need for further laboratory studies that identify the effects of acidification on more species, throughout the entire life cycle, and under realistic environmental conditions. Lacking these further studies, we considered four regimes that bracket the range of possible acidification effects: no effects, strong impacts on benthic invertebrates, moderate impacts on benthic invertebrates, and moderate impacts on benthic invertebrates and plankton. The regime with strong impacts on benthic invertebrates assumed an increased mortality rate of 1% per day for these groups. This drove shallow benthic filter feeders and sea urchins to decline by 83%–90%, respectively, over 20 years relative to their abundance without acidification. The three other benthic shelled groups were driven to extinction. The regimes with moderate impacts on benthic invertebrates assumed an increased mortality rate of less than 0.4%per day, leading these groups to decline by 20%–70%. The regime with moderate effects of acidification for large zooplankton (additional mortality of 1% per day) and small phytoplankton (additional mortality of 30% per day) caused decreases of 75% and 20% in those groups, respectively.

Results

Individual fishing quota catch scenarios

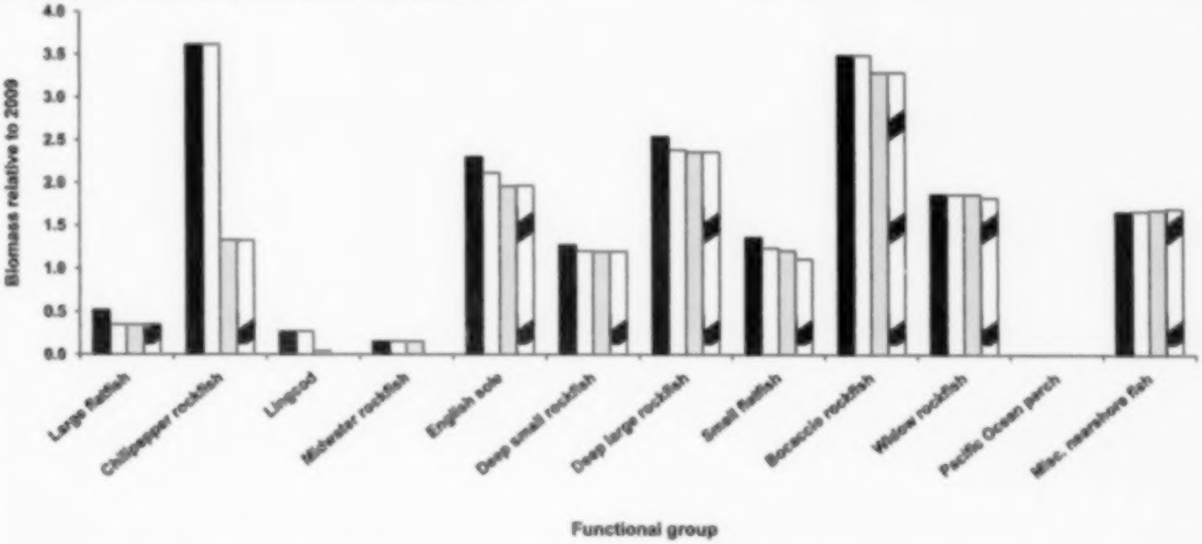
As expected, the scenarios with higher catch of target species led to lower abundances of these species over the course of the simulations (Fig. 2; Table 1). The target species with increased catch included large flatfish (e.g., arrowtooth flounder), chilipepper rockfish, lingcod, midwater rockfish, English sole, deep small rockfish (e.g., longspine thornyhead), deep large rockfish (e.g., shortspine thornyhead), and small flatfish (e.g., Dover sole). Bycatch groups with increased catch included bocaccio, widow rockfish (*S. entomelas*), and Pacific ocean perch.

Over the course of all the 20-year simulations, the abundance of most rockfish and flatfish groups increased (Fig. 2), since the initial conditions of the model are primarily based on biomass estimates from 2000–2007, a period when many of the stocks were beginning to recover from historic overfishing. Several of the species with increased catches also followed this trend, since fishing mortality rates were relatively low. Even in the scenario with the highest total mortality (Scenario 3), the fishing mortality rates are approximately 5% per year for large flatfish (arrowtooth flounder) and 1%–3% for the other target species. For most of these species, the fishing rates considered here accounted for less than a 30% difference in final abundance between scenarios. Exceptions to this were chilipepper rockfish, lingcod, and midwater rockfish, which declined steeply in the scenarios with higher fishing. Chilipepper, lingcod, and midwater rockfish are "underutilized" species that managers aim to target under the IFQ system; IFQs would not change the total allowable catch for these 'underutilized' species, but reduced bycatch rates (e.g., of bocaccio) under IFQs may increase the likelihood that fishers reach the total allowable catch for the underutilized species, rather than being limited by bycatch caps (see supplementary data,[3] Appendix S1). For example, Scenario 3 assumed a chilipepper rockfish catch of 2000 metric tons (mt) compared with 17.8 mt under Status Quo. The additional catch led to final biomasses equal to 37% of their projected biomass under the Status Quo. Midwater rockfish and lingcod both were extirpated in Scenario 3, owing to quota increases of 20-fold and 3-fold, respectively.

The direct effects of fishing presented above are straightforward, and would be captured by single species models that are much simpler than the Atlantis ecosystem model. The motivation for using Atlantis here is that it captures indirect effects related to shifts in predation, which are not represented in single species assessment models. Therefore, we focus more on indirect effects as we present further results from the IFQs and ocean acidification below.

Under the IFQ scenarios, higher levels of fishing led to reduced predation by these target species on their prey. The miscellaneous nearshore fish showed minor increases due to

Fig. 2. Relative abundance (biomass in 2028 / biomass in 2009) for select functional groups. From left to right, for each group, the bars represent the status quo scenario, Scenario 1, Scenario 2, and Scenario 3. The eight target species on the left experience increasing fishing pressure as we shift from the Status Quo scenario towards Scenario 3. Catches of bycatch species (bocaccio and widow rockfish and Pacific ocean perch) also increase from left to right. For miscellaneous nearshore fish, fishing pressure does not vary between scenarios, but differences in predation mortality cause differences in abundance.



this decline in predation (Fig. 2; Table 1). This group, which includes sculpin (Cottidae) and white croaker (*Genyonemus lineatus*), increased by approximately 2%, owing to the reduction in abundance of lingcod. Twenty percent of lingcod diet is composed of these nearshore fish species (Dufault et al. 2009).

We did not see strong indirect effects (>5%) on target or forage species in these particular fishing scenarios. This may be a function of the inherent structure of the food web and ecosystem, but also may be due to the fact that the management scenarios considered here involve low total fishing mortality rates of <5% per year. The small differences in fishing mortality rates between the scenarios translate into small differences in target species biomass, and a limited impact on the other components of the food web.

Scenarios with ocean acidification impacts on benthos

Combining the IFQ catch scenarios with ocean acidification confronted the benthic fish species with a food web that was depleted in shelled benthos, such as bivalves, snails, corals, sea urchins, sea stars, and brittle stars. Our scenarios with strong impacts on shelled benthos resulted in 80%–100% declines in these benthic groups within 20 years, relative to what would be expected without additional mortality due to acidification. Our scenarios with moderate impacts resulted in declines of 20%–70% for these groups (Table 1). We illustrate the impacts of this in two ways: the results for the status quo harvest scenario under each acidification regime are shown (Fig. 3), in terms of stock increase or stock decline relative to initial (~2009) biomasses. Complete results for all simulations are provided (Table 1), but for ease of comparison we have standardized all biomasses relative to the Status Quo scenario without acidification.

The loss of shelled benthic prey groups led to declines primarily in English sole and, to a lesser extent, in small demersal sharks (e.g., spiny dogfish) (Fig. 3; Table 1). Observations from Washington and Oregon suggest that both functional groups derive about 10% of their diets from shelled benthos (Dufault et al. 2009). Rather than doubling in biomass as they did without ocean acidification, with strong acidification and the Status Quo scenario, English sole fell to 40% of initial levels (Fig. 3), and to as low as 6% of initial levels in the more heavily fished scenarios. With moderate acidification, ending biomass was 160%–190% of initial levels, which is approximately 16% lower than would be expected without acidification (Fig. 3, Table 1). The effect of acidification on small demersal sharks was more constrained: without acidification or with only moderate acidification they increased in abundance to about 2.0× initial levels, and with extreme acidification this fell to ~1.9× (Fig. 3).

Three additional impacts of the benthic acidification scenarios were a decline in skates and rays, a slight increase in canary rockfish, and a slight increase in miscellaneous nearshore fish (croakers and sculpins) (Fig. 3; Table 1). Skates and rays declined under acidification, owing to decreases in the abundance of benthic grazers (sea urchins), which are a minor component of skate diet. Strong acidification caused a 30% decline in skates and rays, and moderate acidification caused a 10% decline, relative to the scenario with no acidification (Table 1). Under strong acidification impacts, the biomass of miscellaneous nearshore fish and canary rockfish increased toward the end of the simulations by ~13% and 6%, respectively (relative to the no acidification scenario) owing to the decline in their predator, small demersal sharks (Table 1). These interactions are driven by small (<5%) diet

Table 1. Biomass of functional groups at year 20, for each harvest scenario and acidification regime.

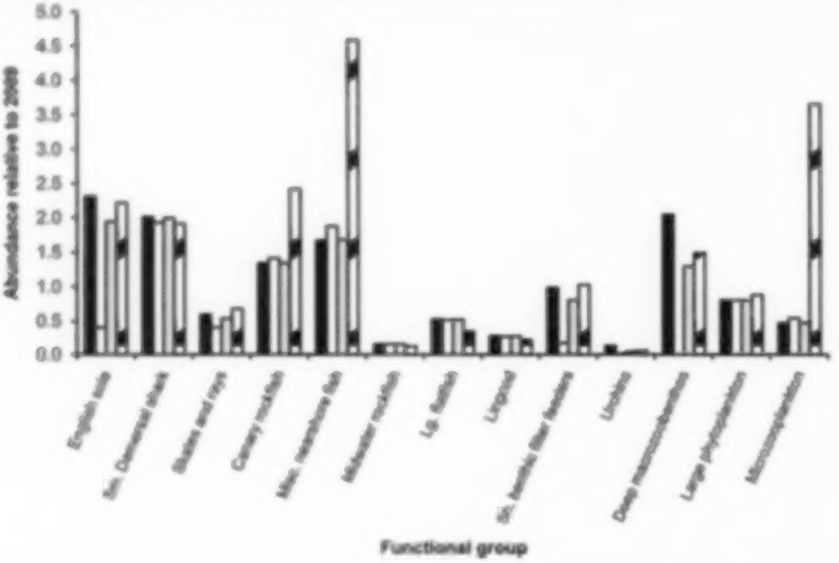
	No ocean acidification				Strong acidification impacts on benthos				Moderate acidification impacts on benthos				Moderate acidification impacts on benthos and plankton			
Functional group	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3
Large planktivores(mackerel)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Canary rockfish	1.00	1.00	1.01	1.01	1.06	1.06	1.07	1.08	1.00	1.01	1.01	1.02	1.80	1.83	1.86	1.89
Small planktivores (sardine, anchovy)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	0.97	0.97	0.97
Large flatfish (arrowtooth)	1.00	**0.67**	**0.67**	**0.68**	0.99	**0.66**	**0.66**	**0.67**	1.00	**0.67**	**0.67**	**0.68**	**0.66**	**0.38**	**0.39**	**0.40**
Chilipepper rockfish	1.00	1.00	**0.37**	**0.37**	1.00	1.00	**0.37**	**0.37**	1.00	1.00	**0.37**	**0.37**	1.00	1.00	**0.37**	**0.37**
Lingcod	1.00	1.00	**0.16**	**0.00**	0.98	0.98	**0.14**	**0.00**	1.00	1.00	**0.16**	**0.00**	**0.78**	**0.78**	**0.00**	**0.00**
Salmon	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Large pelagic predators (tuna)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Shearwaters	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.99	0.99
Hake	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98
Sablefish	1.00	1.00	1.00	1.00	1.03	1.03	1.03	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Deep vert.migrators (myctophids)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.99	0.99
Deep misc. fish (slickhead, eelpout)	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98
Misc. nearshore fish (croaker, sculpin)	1.00	1.01	1.02	1.02	1.13	1.14	1.16	1.17	1.01	1.02	1.02	1.03	2.75	2.81	2.87	2.93
Midwater rockfish	1.00	1.00	1.00	**0.00**	1.01	1.01	1.01	**0.00**	1.00	1.00	1.00	**0.00**	**0.79**	**0.79**	**0.79**	**0.00**
Bocaccio rockfish	1.00	1.00	**0.94**	**0.94**	1.00	1.00	**0.94**	**0.94**	1.00	1.00	**0.94**	**0.94**	1.00	1.00	**0.94**	**0.94**
English sole	1.00	**0.92**	**0.85**	**0.85**	**0.17**	**0.09**	**0.02**	**0.02**	**0.84**	**0.76**	**0.69**	**0.69**	0.96	**0.88**	**0.80**	**0.80**
Shallow small rockfish	1.00	1.00	1.00	1.00	1.02	1.02	1.02	1.02	1.01	1.01	1.01	1.01	0.99	0.99	0.99	0.99
Deep small rockfish (longspine)	1.00	**0.94**	**0.94**	**0.94**	1.00	**0.94**	**0.94**	**0.94**	1.00	**0.94**	**0.94**	**0.94**	1.01	0.95	**0.95**	**0.95**
Deep large rockfish (shortspine)	1.00	**0.94**	**0.93**	**0.93**	1.00	**0.94**	**0.93**	**0.93**	1.00	**0.94**	**0.93**	**0.93**	0.95	**0.89**	**0.88**	**0.88**
Small flatfish (petrale, dover, etc.)	1.00	**0.91**	**0.89**	**0.82**	1.00	**0.91**	**0.89**	**0.81**	1.00	**0.91**	**0.89**	**0.82**	1.03	**0.94**	**0.92**	**0.85**
Small demersal sharks (dogfish)	1.00	1.00	1.00	1.00	0.96	0.96	0.96	0.96	0.99	0.99	0.99	0.99	0.95	0.95	0.95	0.95
Large demersal sharks (sixgill, etc.)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.02	1.02	1.02	1.02
Pacific Ocean perch	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pelagic sharks	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	**0.93**	**0.93**	**0.93**	**0.93**
Shallow large rockfish	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.00	1.00	1.00	1.00	1.05	1.05	1.06	1.06
Skates and rays	1.00	1.00	1.00	1.01	**0.68**	**0.69**	**0.69**	**0.69**	**0.90**	**0.91**	**0.91**	**0.91**	1.15	1.16	1.16	1.17
Surface feed birds (gulls)	1.00	0.99	0.98	0.98	1.03	1.02	1.01	1.01	0.99	0.99	0.97	0.97	0.98	0.97	0.96	0.96
Diving birds	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.03	1.04	1.04	1.04
Pinnipeds	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Transient orcas	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Baleen whales	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Widow rockfish	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.98
Toothed whales	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Otters	1.00	1.00	1.00	1.00	0.98	0.98	0.98	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Squid	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Shallow benthic filter feeders	1.00	1.01	1.02	1.02	**0.17**	**0.17**	**0.17**	**0.17**	**0.82**	**0.82**	**0.83**	**0.83**	1.04	1.05	1.06	1.06
Other benthic filter feeders	1.00	1.01	1.01	1.01	**0.00**	**0.00**	**0.00**	**0.00**	1.86	1.88	1.88	1.88	2.31	2.32	2.32	2.32
Deep benthic filter feeders	1.00	1.00	1.00	1.00	**0.00**	**0.00**	**0.00**	**0.00**	**0.33**	**0.33**	**0.33**	**0.33**	**0.35**	**0.35**	**0.35**	**0.35**
Urchins	1.00	1.00	1.01	1.02	**0.10**	**0.10**	**0.10**	**0.09**	**0.36**	**0.36**	**0.37**	**0.38**	**0.44**	**0.44**	**0.44**	**0.43**

Table 1 (*concluded*).

	No ocean acidification				Strong acidification impacts on benthos				Moderate acidification impacts on benthos				Moderate acidification impacts on benthos and plankton			
Functional group	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3	Stat. Quo	Scen1	Scen2	Scen3
Deep macrozoobenthos	1.00	1.00	1.02	1.01	**0.00**	**0.00**	**0.00**	**0.00**	**0.63**	**0.64**	**0.65**	**0.64**	**0.73**	**0.73**	**0.74**	**0.74**
Large crabs	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	1.00	1.00	1.00	1.00	**0.93**	**0.93**	**0.93**	**0.93**	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
Shrimp	1.00	1.00	1.00	1.00	1.00	1.07	1.07	1.07	1.00	1.00	1.00	1.00	1.07	1.07	1.07	1.07
Large zooplankton (euphausid)	1.00	1.00	1.00	1.00	1.04	1.04	1.04	1.04	1.00	1.00	1.01	1.00	**0.24**	**0.24**	**0.24**	**0.24**
Deposit feeders	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Macroalgae (kelp)	1.00	1.00	1.00	1.00	1.55	1.55	1.54	1.54	1.05	1.05	1.05	1.05	0.98	0.98	0.98	0.98
Seagrass	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Carnivorous infauna	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Gelatinous zooplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.65	2.65	2.62	2.61
Large phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.10	1.10	1.10	1.10
Small phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	**0.81**	**0.81**	**0.81**	**0.81**
Mesozooplankton (copepods)	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.29	1.29	1.28	1.27
Microzooplankton	1.00	1.01	1.01	1.00	1.15	1.18	1.17	1.19	1.01	1.01	1.01	1.01	7.75	7.75	7.73	7.72
Pelagic bacteria	1.00	1.02	1.03	1.03	1.33	1.35	1.38	1.35	1.05	1.07	1.08	1.08	2.40	2.41	2.42	2.42
Benthic bacteria	1.00	1.02	1.08	1.05	1.78	1.81	1.93	1.87	1.11	1.13	1.20	1.17	1.33	1.35	1.41	1.39
Meiobenthos	1.00	1.01	1.06	1.03	1.43	1.44	1.53	1.48	1.06	1.07	1.13	1.09	1.48	1.49	1.58	1.57
Labile detritus	1.00	1.02	1.08	1.05	1.78	1.81	1.94	1.87	1.11	1.13	1.20	1.17	1.33	1.34	1.40	1.39
Refractory detritus	1.00	1.02	1.08	1.03	1.13	1.15	1.22	1.17	1.05	1.07	1.13	1.08	1.15	1.17	1.22	1.18
Carrion	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Dissolved inorganic N	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	**0.00**	1.33	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**

Note: Biomass is relative to biomass at year 20 in the Status Quo harvest + No Ocean acidification simulations. For reference, cells with values less than 0.95 have bold font. Functional groups that went extinct in the Status Quo harvest + No Ocean Acidification are indicated as "—". Stat. Quo, Status Quo scenario; Scen1, scenario 1; Scen2, scenario 2; Scen3, scenario 3.

Fig. 3. Relative abundance (biomass in 2028 / biomass in 2009) for select functional groups. All bars represent scenarios with Status Quo management. From left to right, for each group, the bars represent regimes with no acidification, strong acidification on shelled benthos, moderate acidification on shelled benthos, and moderate acidification on shelled benthos + plankton.



fractions derived from limited field observations, and may be considered more uncertain than the impacts on English sole and small demersal sharks.

Scenarios with ocean acidification impacts on plankton

The scenarios that represented acidification as a decline in plankton affected more groups than did the scenario above that involved a decline in shelled benthic groups. The additional mortality we imposed on large zooplankton and small phytoplankton caused these plankton groups to decline 75% and 20%, respectively, relative to scenarios with no acidification (Table 1). This led to a considerable reorganization of the food web, most easily seen in a comparison of the Status Quo harvest scenarios across all acidification regimes (Fig. 3); other harvest scenarios follow similar patterns (Table 1). The declines in large zooplankton (pteropods) and small phytoplankton (foraminifera and coccolithophores) released large phytoplankton from both grazing and competition, leading to a 10% increase in biomass. The release in grazing pressure by large zooplankton allowed microzooplankton (e.g., ciliates, dinoflagellates, nanoflagellates) to increase to ~8× the abundance that would be expected without acidification. These increases in plankton groups led to strong increases in detritus production and bacterial groups' biomass, subsequently causing increases in shallow benthic filter feeders and benthic detritivores such as sea urchins and deep macrozoobenthos (e.g., brittle stars). Fish groups such as midwater rockfish and large flatfish declined, owing to the loss of large zooplankton (Fig. 3), which comprises 38% and 10% of the diets of these species, respectively (Dufault et al. 2009). One second-order effect was a decline in lingcod, owing to the loss of midwater rockfish as prey. Another second-order effect included increases in canary rockfish and skates and rays, both of which benefited from increased sea urchin abundance and minor increases in shrimp abundance. We observed one third-order effect: miscellaneous nearshore fish increased to ~4.6× initial abundance, owing to declines in their predator, lingcod (Fig. 3).

Evaluating cumulative impacts of fishing strategies and ocean acidification

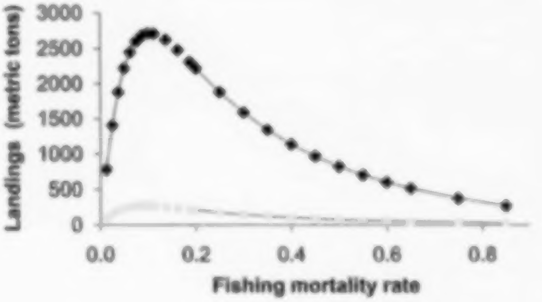
Resource managers may be interested in two aspects of our results, in relation to sustainable use of target fish species and conservation of bycatch species: (*i*) how robust against acidification is the decision to implement IFQs (the decision regarding the overall management system), and (*ii*) how can we evaluate the impacts of acidification in setting harvests for individual species (the decisions regarding specific management policies)?

To evaluate the decision regarding implementation of IFQs, we calculated the relative economic performance of each of the four IFQ scenarios, across each of the ocean acidification regimes. Regardless of the assumptions about acidification, the ranking of landed value summed over all species (tons × price, PacFIN 2008) was Status Quo < Scenario 1 < Scenario 2 < Scenario 3, following the overall pattern of target species landings. Therefore, in terms of total revenue, the Pacific Fishery Management Council's decision to switch to IFQs (Scenarios 1–3) from Status Quo appears robust to acidification. This sort of scenario screening and ranking is one of the strong suits of Atlantis, and ecosystem models in general (Fulton et al. 2007; Plaganyi 2007).

Evaluation of the cumulative impacts of fishing, acidification, and trophic effects can be accomplished using single-species reference points and decision theory (Hilborn and Walters 1992; Quinn and Deriso 1999) that are standard components of fishery management decisions on the US West Coast (e.g., Stewart 2007). As an example, here we focus on English sole, which suffered the most severely of any commercially important species under strong benthic acidification impacts. To give some context, on the US West Coast, 1078 mt of English sole were caught in 2006 (Stewart 2007), with a value of approximately US$700 000; this was approximately one third of the allowable catch set by managers.

Selecting management policies for English sole involves setting quotas based on the status of the stock (depletion) and estimates of the maximum sustainable yield (MSY) and the biomass at which this occurs. These reference points trigger legally mandatory actions; for instance, depleting a stock to less than 25% of unfished biomass necessitates large cuts in harvest and the development of a formal "rebuilding plan" (e.g., MacCall 2008). Using Atlantis analogously to a single species stock assessment, we calculated depletion as the ratio of current spawning stock biomass (SB) to unfished SB. Also analogous to single species assessments, we used two methods to identify MSY: a proxy biomass level (SB = 40% of unfished SB), and direct estimation of MSY and SB_{MSY}. We estimated unfished SB by projecting the Atlantis model for 50 years with no fishing, at which point most species including English sole had increased to quasi-equilibrium levels. Direct estimation of MSY involved fixing the harvest rate at a range of levels, and evaluating catches in year 50 of a 50-year simulation (Fig. 4). We considered the simple case without acidification (i.e., just fishing and trophic effects), and the case with the full cumulative impacts of strong acidification on shelled benthic organisms, fishing, and trophic effects.

Fig. 4. Yield of English sole (*Pleuronectes vetulus*) under various fishing mortality rates (*x*-axis) with current ecological processes (top curve) vs. strong ocean acidification impacts on benthos (bottom curve). Yield is based on catches in year 50 of a 50-year simulation; this is an approximation of an equilibrium sustainable yield.



Our estimated reference points clearly illustrate the dramatic impact of this acidification regime on English sole (Table 2). As current catches are only a third of the quota, there appears to be much scope for a future expansion of catch. However this may not actually be possible, as unfished spawning stock biomass (SB_0) fell by 90% when confronted with strong acidification impacts on benthos. MSY therefore fell 90% as well, regardless of whether we estimated MSY or assumed the $SB_{40\%}$ MSY proxy. The fishing mortality rate corresponding to maximum yield was similar (0.1/year for no acidification and 0.0875/year for strong benthic acidification effects). For comparison, using a single species model, Stewart (2007) estimated single species MSY to be 3452 mt with a fishing mortality rate of 0.13/year, based on a target of 40% of unfished spawning biomass. These results demonstrate that under status quo conditions, our ecosystem model generates similar stock productivity and estimates of fishery reference points as does an "orthodox" single species assessment model for English sole. The main added value of the ecosystem model in this case is that it is able to forecast how the dynamics of the stock change under scenarios with decreased prey abundances due to ocean acidification.

We considered the implications of the four harvest scenarios on the biomass of English sole when the ecosystem involves alternate "states of nature": either no acidification or strong acidification of shelled benthos (Table 3). This approach follows the standard decision table format adopted by US West Coast fishery managers, but adds the full cumulative effects within the Atlantis model. Without acidification, abundance over 20 years under all IFQ scenarios increases relative to initial (2009) abundance; the Status Quo scenario at year 20 even temporarily exceeds the long-term estimate of SB_0. On the other hand, with strong benthic acidification the IFQ catches drive biomass to as low as 7% of initial (2009) abundance; the species appears more depleted even when scaled against the unfished spawning biomass estimated under acidification (SB_{2028}/SB_{0Acid}). This depletion is expected since catch (557–1772 mt) is much greater than our MSY reference points (270 or 260 mt).

Discussion

Though complex simulation models like Atlantis have been successfully used to evaluate management strategies and ecological tradeoffs (Fulton et al. 2007) and in adaptive "gaming" exercises with stakeholders (Christensen and Walters 2004), they are notoriously hard to translate into metrics useful to policy makers. Frequently modelers attempt to summarize the state of the ecosystem using multiple indicators that represent particular components or processes of interest (Fulton et al. 2005; Link 2005). Here we have demonstrated that the messages in these models can also be captured in terms of accepted single-species benchmarks. The potential impact of acidification on unfished biomass (SB_0) and sustainable yield (MSY) of English sole is one example. One of the few similar articles in the literature is by Walters et al. (2005), who calculated MSY for each species in 11 simulated ecosystems, and illustrated interdependence and tradeoffs in sustainable yields of species within each food web. Though natural resource managers increasingly accept ecosystem-based management (EBM) in concept, their day-to-day mandates and their training are usually grounded in single species considerations. Therefore, summarizing cumulative "whole ecosystem" impacts in terms of established reference points and decision mechanisms provides one way to integrate new ecosystem modeling tools with existing scientific and legal frameworks.

Resource managers have implemented individual quotas in many fisheries over the last 20–30 years, including Australia (Young 1999), New Zealand (Annala 1996), Iceland (Arnason 1996), and Alaska (Sigler and Lunsford 2001). In many cases, IFQs have proven to be a successful way to increase the economic and biological performance of fishing industries (Grafton et al. 2006; Costello et al. 2008). In the

Table 2. Management reference points for English sole, based on maximum sustainable yield (MSY) and spawning stock biomass.

	MSY estimated iteratively		MSY based on 40% of SB_0	
Reference point	Status quo	Acidification	Status quo	Acidification
SB_0, unfished spawning biomass (mt)	123 000	15 000	123 000	15 000
MSY (mt)	2 700	270	2 700	260
Spawning stock biomass (MSY; mt)	41 500	4 900	49 100	6 000
Fishing mortality rate (MSY)	0.1	0.0875	0.0875	0.075

Note: MSY was estimated by two methods, both iteratively by testing a range of fishing mortalities, and by using a proxy of 40% of unfished biomass; mt, metric tons.

Table 3. Decision table for English sole evaluating the impact of Status Quo harvest or three alternate Individual Fishing Quota (IFQ) scenarios, faced with either no ocean acidification or strong acidification impacts on benthos.

	State of nature					
	No acidification ($SB_{0NoAcid}$ = 123 000)			Strong acidification on benthos (SB_{0Acid} = 15 000)		
Harvest policy (catch, mt)	SB_{2028}	SB_{2028}/SB_{2009}	$SB_{2028}/SB_{0NoAcid}$	SB_{2028}	SB_{2028}/SB_{2009}	SB_{2028}/SB_{0Acid}
SQ (557 mt)	137 000	2.69	1.12	24 500	0.48	1.63
Scenario 1 (1131)	125 000	2.45	1.02	13 000	0.26	0.87
Scenario 2 (1772)	115 000	2.26	0.94	3 500	0.07	0.23
Scenario 3 (1772)	115 500	2.27	0.94	3 500	0.07	0.23

Note: We simulated harvest policies for 20 years. Results are reported as spawning biomass (SB) at the end of the simulation, relative to 2009 biomass or relative to the appropriate estimate of unfished spawning biomass (SB_0) from Table 2. SQ, status quo; mt, metric tons

British Columbia trawl fishery adjacent to the one modeled here, Branch et al. (2006*b*) found that IFQs, when coupled with full observer coverage and accounting of discards, changed fishing behavior and reduced discards. Our modeling illustrates that as the Pacific Fishery Management Council shifts to an IFQ system, we should not expect past performance to guarantee future results, if the future is dominated by global change. The results shown here suggest that in the absence of ocean acidification the primary impact of IFQ strategies will be on species that are targeted for greatly increased catches, such as chilipepper rockfish. The IFQ harvest scenarios alone will, in most cases, not have strong impacts on the food web, beyond the direct effects on harvested species. This is largely due to fact that the fleet's catches and our scenarios are limited by estimates of optimum yield from stock assessments; harvest on the much larger scale of the 1960s to early 1990s could have had much stronger food web impacts (Field 2004). Most predators and prey of target species were not strongly affected by the scenarios considered here. We observed tradeoffs between lingcod and a primary component of their diets, miscellaneous nearshore fish. Similar indirect effects are commonly evident in multispecies models (e.g., Hinke et al. 2004) and have been observed in the field, particularly in heavily fished systems (Daskalov 2002; Lilly et al. 2000). Given the relatively small differences in fishing mortality associated with the proposed scenarios, it is not surprising that the models predict only minor indirect effects on prey species. Our ecosystem modeling of the food web effects of IFQs is a first step to provide quantitative predictions regarding the ecological impact of IFQs (Branch 2009; Griffith 2008).

Global change, and specifically ocean acidification, may have strong impacts on some target species, separate from what would be expected under a world with IFQs and only fishing effects. The ocean acidification regimes that we considered here range in intensity from no acidification to extirpation of benthic and planktonic shelled organisms. These intensities likely bracket the impacts of declining pH in the world's oceans; in reality, the effects of acidification will ultimately be mediated by competition within functional groups, and species-level characteristics related to shell formation. Previous work by Cooley and Doney (2009) similarly translated projected acidification into 10%–25% declines in mollusks, and equated this to economic losses by US mollusk fisheries of $75–187 million, annually. We have used our ecosystem model to trace the damage from acidification up the food web, revealing that commercially important groundfish stocks such as English sole, arrowtooth flounder (i.e., large flatfish), and yellowtail rockfish (midwater rockfish) are also particularly susceptible to the loss of shelled prey items from their diet. One target species, English sole, exhibited a 10-fold decline in potential catch and economic yield when confronted with strong acidification impacts on shelled benthos. Levin et al. (2006) document that status quo management has resulted in the decline of low productivity rockfish and the increase in more productive species such as flatfish. Thus, the modeled effects of ocean acidification are of concern since they disproportionately affect a portion of the fishery that is productive and currently healthy.

Our work here is only a start toward identifying the implications of ocean acidification on the fishery food web, but it does hint at the important role that the predator/prey response can have on the ultimate effects of acidification on commercial fish stocks. In our modeling, both English sole and small demersal sharks were initialized to have 10% of their diets as shelled benthos, and yet declines in shelled benthos caused much stronger declines in the former than the latter. For English sole, the impact of acidification was increased by a limited supply of alternate prey sources and gape limitation exacerbated by declines in size-at-age. Thus we expect that more modeling and observations of predator diets will be needed to forecast acidification effects, rather than a simple linear response (i.e., a 10% decline if 10% of a predator diet is removed).

The IFQ and acidification simulations presented here are fairly simple. We use projections of total catches, rather than full simulation of fleet dynamics. These projections are meant to capture improvements in targeting with trawl gear, but do not explicitly capture changes in spatial allocation of effort, gear switching, or investment/disinvestment likely to occur to some degree under a trawl IFQ program. The model also lacks management feedback; in reality, fishing mortality rates are not constant, but are adjusted downwards when assessments indicate that the stock has declined below 40% of unfished levels. We ignored discards of species other than groundfish, not only fish but also corals, sponges, and other habitat-forming species. Finally, we should note that the Atlantis modeling framework requires fairly coarse representation of the geography and functional groups. Our fish functional groups typically include 3–4 fish species that in reality are managed separately, while invertebrate functional groups include many genera that may respond differently to acidification.

Our scenarios treated acidification as fixed additional mortality rates on shelled plankton and benthos groups. More detailed modeling of acidification requires coupling global ocean carbon models with empirical studies of calcification rates, as has been done for corals (Kleypas et al. 1999; Guinotte et al. 2003). These authors and others (Fabry et al. 2008) have produced maps predicting decreases in the saturation state of aragonite (a type of calcium carbonate secreted by marine organisms) on a global scale in 50–100 years. The maps suggest decreases in both the area and depths inhabitable by calcifying organisms. Spatially explicit models such as Atlantis can include these projected range contractions, both horizontal and vertical, and can examine the spatial impacts on the food web. For plankton and shelled benthos, a first step might be to assume a fixed effect of acidification only for time periods and areas that have aragonite or calcite saturation states below some generic thresholds (as in Guinotte et al. 2003). A second step, once the necessary empirical studies are available, would relate a gradient of calcite and aragonite saturation states to species' calcification rates and subsequent impacts on population dynamics.

As with any complex simulation model, Atlantis is not intended for making short-term tactical decisions (e.g., annual decisions about total catch limits). Such decisions are best made with single-species stock assessments. For instance, the strong effect of fishing on chilipepper rockfish predicted in our scenarios can be compared to predictions from Field's (2008) stock assessment. In our Scenario 3, sustained catches of 2000 mt/year over 20 years led to biomasses that were 35% of the level expected under negligible fishing (Status Quo). Field (2008) estimated that removing a maximum sustainable yield of 2100 mt would reduce biomass to 46% of unfished levels. Single species models such as Field (2008) are also designed to explicitly estimate parameter uncertainty. The complexity and long run-times of Atlantis prevent the estimation of uncertainty using traditional statistical techniques or sensitivity analyses (e.g., Saltelli et al. 2004); instead, approaches such as bounded parameterization and perturbation analysis can be used to consider both parameter and structural uncertainty (Fulton 2010). Although we would defer to single species models for setting exact quotas or estimating statistical confidence intervals, Atlantis is a useful tool for exercises like the one here, which aim to screen management policies and consider cumulative impacts in addition to fishing. As we have shown, the results can be summarized in terms that have immediate meaning to policy makers.

From the standpoint of balancing local conservation and economic needs, it is perhaps most encouraging that the policy scenarios analyzed here all indicate a fairly low level of fishing mortality on most target species, and a limited impact on predator and prey species. This is indicative of the restrictive total allowable catches implemented over the last ten years, during which time several of the stocks have been managed under rebuilding plans. Arnason (1996) and Branch et al. (2006*a*) emphasize that IFQ programs alone will not reduce overfishing of target stocks or impacts on the ecosystem. Instead these authors argue that IFQs must be matched with conservative total allowable catch limits, monitoring and enforcement, and accounting of discards. We add to these conclusions that the efficacy of any fisheries management system, including IFQs and catch limits, is best evaluated in the context of potential global change. Therefore, it seems prudent to complement IFQs with careful consideration of potential global change effects, active monitoring for such effects, and adaptive policies to adjust catch limits if ocean acidification or other environmental change begin to drive underlying population dynamics.

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The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish

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Abstract: Although the selective pressures of commercial fishing are well known, few studies have examined this phenomenon in recreational fisheries. This study used a unique population of largemouth bass (*Micropterus salmoides*) with lines bred for low (LVF) and high (HVF) vulnerability to recreational angling. We evaluated whether differential vulnerability to angling was correlated with physiological traits, including metabolic rate, metabolic scope, anaerobic capacity, and biochemical response to exercise. Indeed, angling selection affected the metabolic rate of fish significantly. The standard metabolic rate was 10%, maximal metabolic rate was 14%, and metabolic scope was 16% lower for LVF compared with HVF. Following exhaustive exercise, LVF required 1 h for lactate levels to recover to control values, whereas HVF required 2 h. Anaerobic energy expenditure was significantly lower for LVF, a finding consistent with the observation that LVF swam at a steadier rate during exercise. Although the reasons behind vulnerability to angling are complex, the phenotypic trait "vulnerability to angling" appears to be linked to a suite of physiological traits, including metabolism and the capacity for anaerobic activity. Thus, angling-induced selection might alter the physiological characteristics of wild largemouth bass populations, with unknown outcomes for long-term population viability.

Résumé : Bien que l'on connaisse bien les pressions sélectives qui s'exercent dans les pêches commerciales, peu d'études se sont intéressés au phénomène dans la pêche sportive. Notre étude examine une population particulière d'achigans à grande bouche (*Micropterus salmoides*) qui possède des lignées sélectionnées pour leur vulnérabilité basse (LVF) ou élevée (HVF) à la pêche sportive. Nous avons déterminé si les différences de vulnérabilité à la pêche sportive sont en corrélation avec des traits physiologiques, tels que le taux métabolique, le profil métabolique, la capacité anaérobie et la réaction biochimique à l'exercice. En effet, la sélection par la pêche sportive affecte significativement le taux métabolique des poissons. Chez les poissons LVF, le taux métabolique standard, le taux métabolique maximal et le profil métabolique sont respectivement 10 %, 14 % et 16 % plus bas que chez les poissons HVF. Après un exercice épuisant, il faut 1 h pour que les concentrations de lactate retournent aux concentrations témoins chez les LVF, mais il faut 2 h chez les HVF. La dépense énergétique anaérobie est significativement inférieure chez les LVF, un résultat qui est compatible avec l'observation que les LVF nagent à un taux plus régulier durant l'exercice. Bien que les raisons qui expliquent la vulnérabilité à la pêche sportive soient complexes, le trait phénotypique « vulnérabilité à la pêche sportive » semble être relié à une série de traits

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physiologiques et en particulier au métabolisme et à la capacité d'activité anaérobie. Ainsi la sélection exercée par la pêche sportive peut modifier les caractéristiques physiologiques de populations sauvages d'achigans à grande bouche, avec des résultats inconnus sur la viabilité à long terme de la population.

[Traduit par la Rédaction]

Introduction

Selectively harvesting fish populations for economically desirable traits generates directional selection pressures that can lead to evolutionary changes of life-history traits such as age and size at maturation, reproductive investment, or growth rate in heavily exploited stocks (Law 2000; Heino and Godø 2002; Kuparinen and Merilä 2007). Although much of the evidence for fishing-induced selection has been attributed to commercial marine fisheries, the potential also exists for recreational angling to generate similar selection pressures (Cooke and Cowx 2006; Lewin et al. 2006; Philipp et al. 2009). In inland freshwater systems with small, locally adapted stocks, angling mortality may be particularly intense (Post et al. 2002; Arlinghaus and Cooke 2005; Cooke and Cowx 2006). In a manner similar to commercial fishing, recreational angling can also be highly selective for size, species, and sex, but in addition, a suite of physiological and behavioural traits may be under equal or stronger selection pressures than those related to body size (reviewed in Lewin et al. 2006; Uusi-Heikkilä et al. 2008). For example, behaviours linked with size or sex might be under selection in recreationally important fish species, such as aggression in male largemouth bass (*Micropterus salmoides*) during the extended parental care period (Suski and Philipp 2004; Uusi-Heikkilä et al. 2008). Not only is there potential for selection against these traits upon harvest, but selection can also occur in catch-and-release fisheries when fish experience hooking or stress-related mortalities (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007) or physiological impairment of reproductive behaviour (Cooke et al. 2002*b*), which facilitates nest predation and loss of broods in species with nest guarding behaviour such as largemouth bass and smallmouth bass (*Micropterus dolomieu*; Kieffer et al. 1995; Cooke et al. 2002*b*). Limited information exists for the potential of fishing-induced selection to affect behavioural and underlying physiological traits, and this research area has been identified as one of the most pressing areas to advance the field of fishing-induced evolution (Uusi-Heikkilä et al. 2008).

Advances in the understanding of recreational fishing-induced evolution have recently occurred using largemouth bass as a model species. In an experimental population of largemouth bass that were specifically selected for differential vulnerability to angling over three generations, it was determined that vulnerability to angling is a genetically heritable trait (Philipp et al. 2009). Although it has been recognized for some time that certain individuals within a species are more vulnerable to angling than others, for example in largemouth bass (Bennett 1954) and brown trout (*Salmo trutta*) (McLaren 1970), this study was the first to demonstrate a heritable basis for individual differences in vulnerability to the angling gear (Philipp et al. 2009). Explanations for these variable responses have been related to different levels of wariness or boldness, and the differential ability of individual fish to learn from previous experiences (Anderson and Heman 1969; Beukema 1970; Garrett 2002). Alternative possibilities link the amount of nutrients required by fish with spatial and temporal foraging activity as means of encountering anglers' artificial lures more often (Philipp et al. 2009). Indeed, a study by Cooke et al. (2007) demonstrated that lower vulnerability to angling in largemouth bass was correlated with lower resting cardiac variables, which are measures known to approximate standard metabolic rate (SMR) (Satchell 1991). SMR represents the minimum energy demand for baseline organismal function (Fry 1957), and lower rates are less energetically costly (Brett and Groves 1979). It is conceivable that any decreases in demands for foraging activity for obtaining resources make these fish less susceptible to capture by anglers. If SMR is a driving force behind differential vulnerability to angling, behavioural differences and activity rates may also emerge as important traits correlated with metabolism or other physiological properties of the individual fish (Uusi-Heikkilä et al. 2008).

In physiologically stressful situations, fish can be exposed to anaerobic disturbances (Booth et al. 1995; Cooke et al. 2002*b*) that result in the depletion of muscle glycogen, adenosine triphosphate (ATP), and phosphocreatine (PCr) stores, as well as the production of lactate (Driedzic and Hochachka 1978; Milligan 1996). The severity of anaerobic disturbance can be determined during simulated exhaustive exercise (Milligan 1996; Kieffer 2000). In addition, an indication of overall anaerobic (i.e., lactate dehydrogenase (LDH)) and aerobic (i.e., citrate synthase (CS) and, cytochrome *c* oxidase (CCO)) capacity can be gained from muscle enzyme activity (Somero and Childress 1980; 1990). The duration of recovery has implications for the resumption of aerobic activity (reviewed in Goolish 1991). An evaluation of exercise performance, recovery, and muscle enzyme activities of fish differentially selected for vulnerability to angling may provide additional insight into the physiological traits under selection, as well as the potential consequences of fishing-induced selection for wild fish stocks.

The purpose of this study was to evaluate the physiological correlates of vulnerability to angling in two experimental lines of largemouth bass that were differentially selected for this trait, and that exhibit rather dramatic differences in catchability to rod-and-reel angling (Philipp et al. 2009). In fact, angling vulnerability was determined to be a heritable trait with a heritability of about 0.15 (Philipp et al. 2009). Specifically, we tested the hypothesis that low vulnerability fish (LVF) and high vulnerability fish (HVF) would have different metabolic rates and scopes. In terms of predictions, first based on previous findings where LVF had lower resting cardiac variables (Cooke et al. 2007), we predicted that LVF would display a lower SMR than would HVF. Second, because fish with a lower SMR should correspondingly decrease their maximum metabolic rate (MMR; Priede 1985), we predicted that LVF and HVF would have comparable metabolic scopes. We also tested the hypothesis that LVF and HVF would have a different physiological response to exhaustive exercise. Based on the expectation that LVF would display a lower SMR with decreased energetic demands (Priede 1985), we predicted that LVF would have a reduced anaerobic capacity, as indicated by muscle lactate dehydrogenase (LDH), and accumulate less lactate than HVF. LVF would then be expected to require proportionally less time to recover from exhaustive exercise (Goolish 1991).

Materials and methods

Study animals

This study takes advantage of an artificial truncation selection experiment that began several decades ago at the Illinois Natural History Survey in the USA (Philipp et al. 2009). Beginning in 1977, largemouth bass in Ridge Lake (Illinois, USA, 39.40°N, 88.16°W; 7.1 ha surface area) were subjected to four consecutive seasons of angling, and catch histories of tagged individuals were recorded as part of a project evaluating the impact of catch-and-release angling (Burkett et al. 1986). Following these four seasons of angling, the reservoir was drained and the largemouth bass were collected. Based on an assessment of individual catch histories, two divergent experimental lines, each with two replicate lines, were selected for low and high vulnerability to angling (Philipp et al. 2009). Low vulnerability brood fish (LVF) were never captured across all four seasons, and high vulnerability brood fish (HVF) were captured more than four times in a single season (Philipp et al. 2009). Five pairs in each parental (P1) generation of each line were bred in separate experimental ponds to produce first (F1) generation offspring, which were then differentiated by pelvic fin clips (Philipp et al. 2009). The offspring from each replicated line ($N = 200$) were raised together in a common pond for three years until the individuals were large enough to be angled (Philipp et al. 2009). A selection procedure using experimental angling over one season was repeated on the F1 fish, and artificially selected LVF and HVF based on catch frequency were again separated into different experimental ponds for breeding (Philipp et al. 2009). The F2 generation offspring were raised in a manner similar to the F1 generation, and the same selection procedure was repeated until the F4 generation. The response to selection was found to increase with each generation, and LVF displayed a heightened response as compared with HVF (Philipp et al. 2009). The fish used in the current study were bred naturally in ponds in the spring of 2006 from the F3 generation, and they had not experienced any further artificial selection.

Oxygen consumption and metabolic rates

In October 2007, a sub-sample of juvenile LVF and HVF were removed randomly from a common experimental pond at the University of Illinois in Champaign–Urbana and transported to the Kaskaskia Biological Station, near Sullivan, Illinois (39.60°N, 88.61°W). There were no significant differences between the weights for the two groups [LVF, 95.0 ± 6.7 g (mean ± standard error of the mean, SEM) ($N = 8$); HVF, 78.8 ± 8.3 g ($N = 8$); $P = 0.15$], but there was a significant difference between the total lengths (LVF, 200 ± 4.0 mm; HVF, 172 ± 11.4 mm; $P = 0.04$). Prior to experimentation, all fish were held for a minimum of 60 h in a recirculating tank (~300 L) at water temperatures of 20 ± 0.8 °C, dissolved oxygen levels of 8.2–8.8 $mg\cdot L^{-1}$, ammonia levels of less than 3.0 ppm, a pH of 7.6, and a natural photoperiod (12 h light : 12 h dark). The fish were not fed for the duration of the experimental trials, which lasted for one week.

Oxygen consumption (standard metabolic rate, SMR) of the two lines was measured using computerized, intermittent flow-through respirometry (Loligo Systems, Tjele, Denmark) with a configuration similar to that described by Herskin (1999). Briefly, four glass chambers (volume = 0.7 L) were immersed side by side in a 175 L tank maintained at 20.5 ± 1 °C. The water in the tank was aerated and filtered continuously through charcoal and a UV-sterilizer. Water was recirculated continuously through each chamber using small fountain pumps, which were driven by AutoResp™ 4 software (Loligo Systems, Tjele, Denmark) installed on a personal computer. The system alternated between a 5 min closed, re-circulating measurement phase, a 4 min open flushing phase, with a 1 min delay period (Herskin 1999).

Variations in oxygen partial pressures (Po_2) were measured by fiber optic oxygen probes connected to an OXY-4 fiber optic oxygen instrument (Loligo Systems, Tjele, Denmark). Po_2 was recorded every second during the 5 min measuring phase, and a linear regression was calculated between Po_2 and time. The slope of the regression line (k) was used to calculate oxygen consumption according to the equation:

$$Mo_2 = kV_{resp}\cdot M^{-1}\alpha,$$

where Mo_2 is the oxygen consumption in mg $O_2\cdot kg^{-1}\cdot h^{-1}$, V_{resp} is the volume of the respirometry chamber in L, M is the fish mass in kg, and α is the solubility of O_2 in water at the experimental temperature (Cruz-Neto and Steffensen 1997). All slopes used in the calculations were derived from equations where $r^2 > 0.95$. This method generated one Mo_2 data point every 10 min.

Experimental trials consisted of placing two LVF and two HVF in individual chambers during the afternoon. The fish were left undisturbed for an afternoon and an overnight period (18–20 h), during which time the AutoResp™ 4 software controlled the measuring and flushing phases and recorded Mo_2. SMR was determined for each individual fish by averaging the lowest six Mo_2 values recorded between approximately 2100–0800, and is representative of a 1 h period (McKenzie et al. 2003). Routine metabolic rate (RMR) was determined by averaging the six Mo_2 values recorded between approximately 1845–1945, after the fish had acclimated to their chambers and had resumed normal daylight activities.

Upon completion of the SMR trials, the elevation of Mo_2 following exercise was assessed, generating a factor similar to "excess post-exercise oxygen consumption" (EPOC; Gaesser and Brooks 1984), which enabled us to evaluate recovery patterns. Previous work has used swimming respirometry and the continuous monitoring of recovering fish over time to generate data on MMR and EPOC (Jain et al. 1998; Farrell 2007). However, largemouth bass are regarded as poor swimmers, and their lifestyle is more consistent with a "sit-and-burst" approach to movement (Kieffer and Cooke 2009). In the current study, we calculated EPOC in a manner that allows a relative comparison of the metabolic scope devoted to recovery following exhaustive exercise. As such, our approach yielded an approximation of EPOC and it was not possible to calculate the area under the curve (as per Farrell 2007) given our protocol. For this measurement, the largemouth bass were individually removed from their chambers and placed in an aerated tank (~60 L), where they were forced to exercise for 2 min by having their tails pinched to induce burst swimming. Tail pinching is a standard method of exhaustively exercising fish to generate physiological disturbances (Wood 1991; Wang et al. 1994). Largemouth bass exhaust quickly relative to salmonids (Kieffer and Cooke 2009), so the 2 min exercise period was considered a substantial metabolic challenge for the fish. Following the 2 min exercise period, the largemouth bass were immediately returned to their chambers and their oxygen consumption rates were recorded over a 2 h period. The highest $M\text{O}_2$ value recorded during the post-exercise period was used as a measure of the MMR for each individual. Metabolic scope was calculated as the difference between the MMR and the lowest $M\text{O}_2$ measured overnight. For the 2 h recovery period, the EPOC values were expressed as a percentage of the metabolic scope calculated at 30 min intervals with an initial 15 min value.

Exercise and muscle metabolites

In July 2007, a random sub-sample of LVF and HVF were removed from an experimental pond at the University of Illinois in Champaign–Urbana and transported to the Sam Parr Biological Station near Kinmundy, Illinois (38.77°N, 88.85°W). There were no significant differences between the weights for the two groups [LVF, 13.3 ± 0.4 g (mean ± SEM) (N = 49); HVF, 12.7 ± 0.2 g (N = 47); P = 0.14], but there was a significant difference between the total lengths (LVF, 110 ± 0.9 mm; HVF, 106 ± 0.6 mm; P = 0.002). Prior to experimentation, fish were held for a minimum of 48 h in recirculating tanks (~600 L) at a density of 7–8 fish per tank. Water temperatures in the tanks were 23–24.5 °C, dissolved oxygen levels were 8.2–8.5 mg·L^{-1}, ammonia levels were less than 0.25 ppm, and a natural photoperiod (14 h light : 10 h dark) was maintained. These fish were not fed for the duration of the experimental trials, which lasted 10 d.

To generate control (resting) physiological values, individual LVF and HVF were removed from the holding tanks and placed in darkened holding chambers (0.8 L) continuously supplied with aerated water. Fish were left undisturbed for a 24 h period, at which time a lethal dose of anesthetic (250 mg·L^{-1} of tricaine methanesulfonate buffered by 500 mg·L^{-1} of sodium bicarbonate) (Summerfelt and Smith 1990) was introduced into the chamber. Once fish had completely lost all reactivity (~2 min), all white muscle above the lateral line and behind the operculum (~1 g) was removed using a razor blade. Muscle samples were immediately freeze-clamped with aluminum tongs pre-cooled in liquid nitrogen and then stored in liquid nitrogen until processing (Booth et al. 1995).

To induce a physiological disturbance, an exhaustive exercise regime was applied to another group of LVF and HVF. Fish were transferred from a common holding tank to an aerated circular container (20 L) where they were chased by tail pinching for 2 min. Following the 2 min exercise regime, one group of fish (both LVF and HVF) was immediately transferred into a solution of buffered anesthetic (2 L) for euthanization and white muscle samples were removed as previously described. Three additional groups of largemouth bass (both LVF and HVF) were also exercised for 2 min and then placed into individual holding chambers and allowed to recover for 1, 2, or 4 h. Following the recovery period, buffered anesthetic was introduced into each chamber for euthanization and white muscle samples were removed as described above.

Tissue metabolite assays

White muscle tissue was prepared for metabolic assays by following the methods of Booth et al. (1995). Briefly, 0.5 g of frozen muscle was ground under liquid nitrogen using a mortar and pestle. The powdered tissue was first combined with a solution of 8% perchloric acid and 1 mmol·L^{-1} ethylenediaminetetraacetic acid (EDTA), and then with a volume of neutralizing solution (containing 2 mol·L^{-1} potassium hydroxide, 0.4 mol·L^{-1} potassium chloride, and 0.3 mol·L^{-1} imidazole). The resulting supernatant was stored at –80 °C to be assayed later. Analyses of tissue lactate, PCr, and ATP concentrations were performed in duplicate on the prepared muscle extracts using the enzymatic assay techniques of Lowry and Passonneau (1972). Water content of the muscle samples was determined as outlined in Suski et al. (2003).

The total anaerobic energy expenditure (AEE) in the white muscle of fish from each exercise treatment group was expressed in terms of ATP equivalents according to the following equation:

$$\text{AEE} = (\Delta\,\text{lactate} \times 1.5) + \Delta\text{ATP} + \Delta\text{PCr},$$

where Δ represents the difference between control and exercise values, 1.5 units of ATP are generated per unit of lactate, and 1 unit of PCr is equal to 1 unit of ATP (Pearson et al. 1990; McDonald et al. 1998*a*).

Tissue enzyme and protein assays

White muscle samples from a separate group of control (no exercise) fish were prepared for enzymatic assays using the homogenization technique described in Rajotte and Couture (2002). The homogenization buffer contained 20 mmol·L^{-1} 4-(2-hydroxyethyl)-1-piperazine ethanesulfonic acid (HEPES), 1 mmol·L^{-1} EDTA, and 0.1% Triton X-100. All enzyme activity determinations were performed in duplicate at 24 °C (the optimum temperature for growth of largemouth bass) using a UV/Vis spectrophotometer (Varian Cary 100, Varian Inc., Palo Alto, California, USA). Tissue dilutions and cofactor concentrations were selected from assay optimizations. Enzyme assays were conducted (in the following order) for citrate synthase (EC 4.1.3.7; CS), lactate dehydrogenase (EC 1.1.1.27; LDH), and cytochrome *c* oxidase (EC 1.9.3.1; CCO). The wavelengths and millimolar

Table 1. Metabolic rates ($mg\,O_2 \cdot kg^{-1} \cdot h^{-1}$) and body weight (g) for high vulnerability (HVF) and low vulnerability (LVF) largemouth bass, presented as mean ± SEM.

Parameter	Vulnerability line		Test statistic	*P* value
	HVF	LVF		
Body weight	79±8.3	95±6.7	T = –1.53	0.15
Standard metabolic rate (SMR)	115±3.6	104±3.3	T = 2.42	0.029
Maximal metabolic rate (MMR)	280±11.8	241±7.5	T = 2.85	0.014
Metabolic scope	167±9.4	140±6.0	T = 2.51	0.026
Routine metabolic rate (RMR)	189±26.5	130±3.0	U = –0.95	0.35

Note: N = 8 for all values, except metabolic scope for HVF, where N = 7. T denotes the use of a *t* test, and U denotes the use of a Mann–Whitney *U* test.

extinction coefficients identified for CS, LDH, and CCO were identical to those used in Couture et al. (1998), with the exception of the millimolar extinction coefficient for cytochrome *c*, which was 18.7. The reactions were linear over the 5 min period used for the calculation of enzyme activity, and the results are expressed in international units (micromole of substrate converted to product per minute) per gram of tissue mass. Assay conditions for CS, LDH, and CCO were as described in Pelletier et al. (1994), with the following modifications. For LDH, 0.16 $mmol \cdot L^{-1}$ nicotinamide adenine dinucleotide reduced (NADH) and 1.0 $mmol \cdot L^{-1}$ pyruvate were used; and for CS, 0.1 $mmol \cdot L^{-1}$ acetyl CoA and 0.15 $mmol \cdot L^{-1}$ oxaloacetate were used. For CCO, the pH was adjusted to 7.5. The protein content of the muscle extracts was determined using the bicinchoninic acid method of Smith et al. (1985) with bovine serum albumin as a standard.

Statistical analyses

Normality was assessed using a one-sample Kolmogorov–Smirnov test, and homogeneity of variance was assessed using the Levene's test. Comparisons were made between LVF and HVF for SMR, MMR, RMR, metabolic scope, and tissue enzymes using *t* tests. Where the assumption of equality of variance was not met, the nonparametric Mann–Whitney *U* test was used. An arcsine square-root transformation was carried out on EPOC data, because they were expressed as a percentage of metabolic scope. These EPOC values were compared between LVF and HVF across recovery periods using a two-way repeated measures analysis of variance with individual fish entered as a random effect, and both treatment and recovery time entered as fixed effects. The mean concentrations of tissue metabolites and anaerobic energy expenditures were compared between LVF and HVF across recovery periods using a two-way analysis of variance (ANOVA; main effects: vulnerability group and recovery time). For the two-way ANOVAs, when there was a significant difference between HVF and LVF coupled with a significant treatment effect but no significant interaction, a post hoc *t* test was used to identify differences between HVF and LVF. For situations following the two-way ANOVA with no significant HVF/LVF effect, no significant interaction, but a significant treatment effect, a Tukey–Kramer honestly significant difference (HSD) post-hoc test was used to compare individual recovery times with each other (independent of HVF/LVF effects). For situations following the two-way ANOVA with a significant interaction combined with a significant group and (or) treatment effect, data were split and examined within lines with a Tukey–Kramer HSD post-hoc test to identify differences within lines at different recovery points (Sokal and Rohlf 1995). For the two-way ANOVAs involving muscle metabolites, EPOC, and AEE, all models were initially run independently with individual fish weight and length as covariates; because neither of these covariates had a significant influence on the dependent variable in any case, length and weight were omitted from subsequent models reported below. All *t* tests were carried out using SPSS 11.0 (SPSS Inc., Chicago, Ill.). All ANOVAs were carried out using JMPIN 7.0.1 (SAS Institute Inc., Cary, North Carolina). Values are reported as means (± SEM), and the level of significance (α) used for all tests was 0.05.

Results

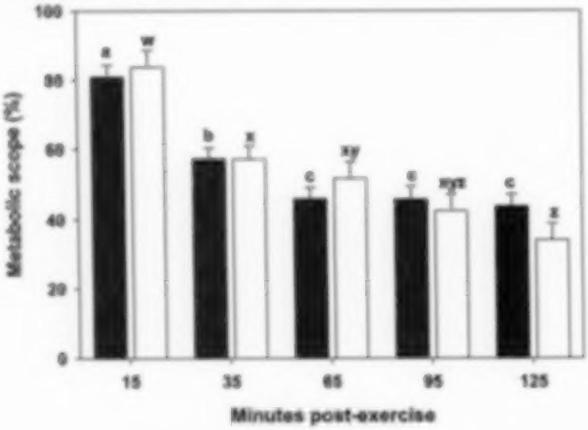
LVF and HVF differed significantly in terms of mass-specific SMR and MMR. SMR was 10% lower and MMR was 14% lower for LVF than for HVF (Table 1). The metabolic scope was approximately 16% lower for LVF than for HVF (Table 1). An initial comparison of RMR between LVF and HVF revealed a 31% lower value for LVF than for HVF. Owing to substantially unequal variances between the RMR for LVF and HVF (Levene's test, $P < 0.05$), a nonparametric test was conducted, which was nonsignificant (Table 1).

Within 15 min after achieving maximal $\dot{M}O_2$, both LVF and HVF were devoting 80%–84% of their metabolic scope to recovery (Fig. 1). The amount of the metabolic scope utilized for EPOC declined to 57% at the 35 min recovery interval, where it then remained relatively stable (within 34%–52%) for the duration of the recovery period (Fig. 1).

During the 2 min exercise trials, differential swimming patterns were observed between HVF and LVF. Upon being chased by tail grabbing, HVF exhibited rapid and erratic burst swimming, whereas LVF did not burst swim as readily. HVF also appeared to reach exhaustion (in terms of being unable to respond to chasing) quicker than LVF. LVF were more often able to sustain some degree of swimming for the duration of the exercise period, although they failed to burst swim with the same vigour as HVF.

Immediately following exhaustive exercise, white muscle ATP and PCr concentrations for both LVF and HVF decreased by 80%–100% relative to resting control values (Figs. 2*a* and 2*b*; Table 2). Owing to variability between individuals, however, differences across treatment groups were not statistically significant. Following 1 h of recovery, tissue

Fig. 1. Percent of metabolic scope utilized during recovery from exhaustive exercise by high vulnerability (HVF) and low vulnerability (LVF) largemouth bass. Filled bars represent HVF and open bars represent LVF. Values are mean ± SEM, where $N = 7$ for HVF and $N = 8$ for LVF. The effects tests for the two-way repeated measures ANOVA are as follows: group, df = 1, $F = 0.002$, $P = 0.97$; treatment, df = 4, $F = 134.6$, $P < 0.001$; interaction, df = 4, $F = 4.5$, $P = 0.003$. Dissimilar letters a, b, and c denote significant differences between pairs of HVF across recovery times, and dissimilar letters w, x, y, and z denote significant differences between pairs of LVF across recovery times (Tukey–Kramer honestly significant difference test, $P < 0.05$).



ATP concentrations were approaching control values for LVF and HVF, and they returned to control levels following 2 h of recovery (Fig. 2*b*; Table 2). Following 1 h of recovery, tissue PCr concentrations had returned to control values and remained there for the entire recovery profile (Fig. 2*a*; Table 2). Mean water content of the white muscle was 78.5% (range 71.0%–81.5%) and did not differ significantly across the different treatments, time periods, or their interaction ($P > 0.05$). Exhaustive exercise for 2 min resulted in an increase in tissue lactate that was 3.5× greater than resting control values for LVF (Fig. 2*c*; Table 2). For HVF, there was a six-fold increase in tissue lactate concentrations over control values (Fig. 2*c*; Table 2). By 1 h following exercise, the tissue lactate concentrations for LVF were no longer significant from resting control values (Fig. 2*c*; Table 2). By 2 h following exercise, tissue lactate concentrations for both LVF and HVF had returned to resting control values, where they remained for the remainder of the recovery profile (Fig. 2*a*; Table 2).

At all measurement points following the exhaustive exercise protocol, the AEE for LVF was significantly lower than the AEE for HVF (Fig. 3). White muscle AEE declined with recovery times, and there was no significant interaction between recovery time and angling vulnerability (Fig. 3; Table 2).

The activity of LDH, an indicator of anaerobic capacity, did not differ between LVF and HVF, nor did the activities of CS and CCO, which are indicators of aerobic capacity (Table 3). Power analyses revealed that the values for β were very low, with the highest reported value at about 0.2 for CCO (Table 3).

Fig. 2. Concentrations of (*a*) PCr, (*b*) ATP, and (*c*) lactate in the white muscle of high vulnerability (HVF) and low vulnerability (LVF) largemouth bass following exhaustive exercise and recovery. Filled bars represent HVF and open bars represent LVF. Values are mean ± SEM, with the sample size for each treatment shown on the bars. For PCr and ATP, differences at individual recovery periods (independent of vulnerability) are denoted by upper case letters joined by a horizontal line (two-way ANOVA), Tukey–Kramer honestly significant difference (HSD) test, $P < 0.05$). For lactate, differences between a recovery period and the within-line control group are indicated by a plus sign (+) for HVF, and an asterisk (*) for LVF line (two-way ANOVA, Tukey–Kramer HSD test, $P < 0.05$). ANOVA results are shown in Table 2.

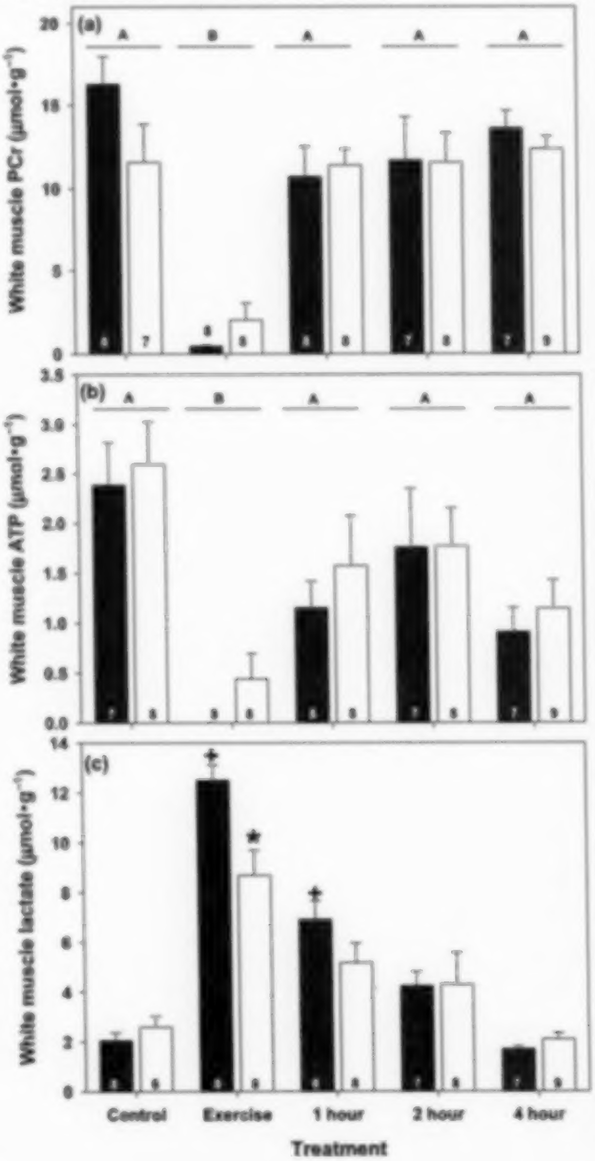
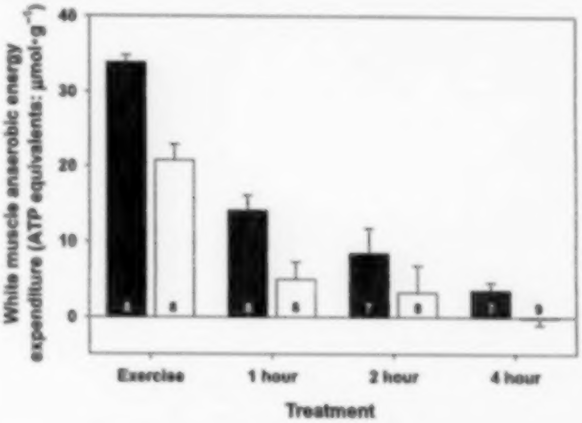


Table 2. Effects tests for two-way ANOVAs used to compare tissue metabolites for high vulnerability (HVF) and low vulnerability (LVF) largemouth bass.

Source	df	*F* ratio	*P* value
Lactate			
Group	1	3.56	0.064
Treatment	4	44.4	<0.01
Interaction	4	3.12	0.021
ATP			
Group	1	1.27	0.26
Treatment	4	10.5	<0.01
Interaction	4	0.11	0.98
PCr			
Group	1	0.63	0.43
Treatment	4	23.1	<0.01
Interaction	4	1.27	0.29
AEE			
Group	1	24.9	<0.0001
Treatment	3	53.1	<0.0001
Interaction	3	1.8	0.15

Note: Body weight was excluded from the final model because it was a nonsignificant co-variate ($P > 0.05$). Group refers to HVF and LVF, and treatment refers to the recovery period following exhaustive exercise.

Fig. 3. White muscle anaerobic energy expenditure (AEE) for high vulnerability (HVF) and low vulnerability (LVF) largemouth bass following exhaustive exercise and recovery. AEE was significantly higher for HVF by comparison with LVF. Filled bars represent HVF and open bars represent LVF. Values are mean ± SEM, with the sample size for each treatment shown on the bars. ANOVA results are shown in Table 2. The effects tests for the two-way ANOVA are as follows: group, df = 1, $F = 24.9$, $P < 0.0001$; treatment, df = 3, $F = 53.1$, $P < 0.001$; interaction, df = 3, $F = 1.8$, $P = 0.15$.



Discussion

Following three generations of artificial selection for differential angling vulnerability, differences in metabolic capacity were observed between two experimental lines of largemouth bass. LVF were found to exhibit a lower SMR than HVF, a trend that is consistent with the lower cardiac output and heart rate found for LVF by Cooke et al. (2007). The combination of a lower SMR and a lower MMR following exhaustive exercise limited LVF to a narrower metabolic scope than HVF. This finding is in contrast to the broader cardiac scope found for LVF by Cooke et al. (2007), where cardiac output and heart rate were used to approximate metabolic scope. The relationship between heart rate and oxygen consumption (used here to determine metabolic rates) is not always linear or constant within a single species, and the relationship can be further confounded by stress (potentially induced by the cardiac surgery) and environmental factors (Thorarensen et al. 1996). It is generally accepted that fish compensate for a higher SMR by increasing their MMR sufficiently to maintain metabolic scope (Priede 1985); however, a higher SMR is known to be more energetically costly and thereby requires a greater food intake (Brett and Groves 1979). It is possible that LVF have acquired a lower metabolic scope in response to the decreased foraging activities necessary to meet their lower energetic demands (Priede 1985), which have been estimated to be 30% lower than those of HVF (Cooke et al. 2007). A study with a population of three-spined sticklebacks (*Gasterosteus aculeatus*) offers support for this argument: the resident, nonmigratory morph displayed a lower SMR, a lower active MR, and a narrower metabolic scope than the active, migratory morph (Tudorache et al. 2007). Under food limited situations the lower SMR might actually be beneficial for LVF and result in elevated growth rate over growth by HVF. This prediction agrees with a study by Redpath et al. (2009) on juvenile LVF and HVF. In that study LVF in ponds were found to grow faster than HVF, which on first sight might seem counterintuitive but can be explained by the lower metabolic costs that LVF have compared with HVF fish. Metabolic scope can also be an indicator of the potential range for aerobic activity (Priede 1985), and an enhanced scope can assist in recovery after burst-type anaerobic activity (Killen et al. 2007). Despite the larger metabolic scope displayed by HVF, both groups devoted nearly identical proportions of their scopes to facilitate recovery from exhaustive exercise and to repay oxygen debts. When not forced to function at the limit of their aerobic capacity, a greater scope may still enable HVF to sustain energetically costly behaviours, such as parental care, better than LVF.

The differences in metabolic capacities measured for largemouth bass selected for differential vulnerability to angling were accompanied by key changes in exercise performance. While the overall trends observed for LVF and HVF in terms of the tissue metabolite (lactate) and energy stores (ATP and PCr) following exhaustive exercise were comparable with results in the literature (reviewed in Milligan 1996), there were some notable variations. Following 1 h of recovery from exhaustive exercise, the lactate levels in LVF had returned to control values, while the lactate levels in HVF were still significantly higher than control values. LVF also demonstrated an AEE that was 39% lower than HVF. AEE is regarded as a measure of realized anaerobic capacity (McDonald et al. 1998*b*), because it encompasses the maximal amount of lactate production and depletion of the tissue energy stores. The swimming behaviour of LVF during the exercise simulation also differed from that of HVF. We observed qualitatively that HVF engaged in higher incidences of burst swimming accompanied

Table 3. Enzyme activities (IU, expressed as g-wet mass^{-1}) and protein concentrations (mg·g^{-1}) for high vulnerability (HVF) and low vulnerability (LVF) largemouth bass, presented as mean ± SEM, where $N = 8$.

	Vulnerability line					
Parameter	HVF	LVF	Test statistic (T)	*P* value	Power (*β*)	Least significant *N*
Lactate dehydrogenase	105.8±7.1	95.3±11.7	0.77	0.46	0.11	54
Citrate synthase	1.96±0.15	2.12±0.22	–0.59	0.57	0.08	91
Cytochrome *c* oxidase	1.51±0.08	1.71±0.15	–1.20	0.25	0.20	23
Proteins	162.8±4.2	155.3±9.5	0.73	0.48	—	—

Note: Least significant *N* represents a power of $\beta = 0.5$; (T) indicates the use of a *t* test.

by faster startle responses, whereas LVF maintained a steadier swimming pattern during manual chasing. These observations, along with the recovery rates for lactate and AEE, suggest that LVF have a lower anaerobic capacity than HVF. Given that the predation strategy of largemouth bass involves a series of short chases with fluctuating swimming velocities (Winemiller and Taylor 1987), this apparent difference in burst swimming ability should allow HVF to capture prey, and hence anglers' lures, more efficiently (Somero and Childress 1980). By contrast, decreased burst swimming ability in LVF may hinder juveniles in their efforts to avoid predators (Fuiman and Magurran 1994), and adult male LVF may not be equipped to defend their broods from predation as well as HVF (Cooke et al. 2002*a*).

Despite the decreased anaerobic capacity and burst swimming ability of LVF, not all of the physiological variables were strongly associated with differential vulnerability to angling, which is consistent with a growing body of literature that challenges the relationship between enzyme capacity and swimming performance (e.g., Gibb and Dickson 2002). Specifically, anaerobic and aerobic enzyme activities and tissue energy stores (ATP and PCr) across the recovery profile were statistically similar for both experimental lines. LDH is an enzymatic indicator of anaerobic capacity (Somero and Childress 1980; 1990), because it is responsible for the conversion of pyruvate to lactate and thus the anaerobic production of ATP (Driedzic and Hochachka 1978). There was no statistical difference between LVF and HVF in terms of LDH activity. Additional enzymes assist in generating anaerobic metabolic power (Somero and Childress 1980) and could be related to the decreased anaerobic capacity observed in LVF. Glycogen stores and the overall glycolytic capacity to produce pyruvate can also influence anaerobic power (Somero and Childress 1990). Although the enzymatic activity of LDH did not provide evidence of a lower anaerobic capacity for LVF, perhaps the decreased AEE in LVF can be related to the availability of less glucose or the activities of enzymes near the beginning of the glycolytic pathway.

An indication of aerobic capacity is provided by CCO and CS, and these enzymes also influence recovery rate (Somero and Childress 1980; 1990). No significant differences were observed between LVF and HVF for the enzyme activities of either CCO or CS. The oxidation rate of lactate into glycogen in the white muscle following exercise is controlled by the mitochondrial enzyme CCO (Goolish 1991), and it is a good indication of recovery rate in terms of lactate clearance (Somero and Childress 1980; 1990). LVF appear to have cleared lactate more quickly, as this metabolite returned to control values with 1 h, by comparison with the 2 h required by HVF. The potential for a higher aerobic capacity in LVF is further supported by the observations of their sustained swimming ability. However, the similarities between the aerobic enzymatic indicators in the two groups of fish make any conclusions difficult. A clear distinction has been made between the initial anaerobic response to exhaustive exercise for LVF and HVF, although further studies are required to determine whether the aerobic capacities are also different between the two strains of fish. Despite the questions that remain unanswered, this study provides evidence that experimental lines of largemouth bass intentionally selected for low and high vulnerability to angling exhibit differences in physiological capacity.

This study provides evidence that vulnerability to angling, a partially genetic trait (Philipp et al. 2009), may be related to a suite of physiological, and possibly behavioural, traits. Vulnerability to angling has been demonstrated to be a genetically heritable trait ($h^2 = 0.15$) for the largemouth bass used in this study (Philipp et al. 2009). The physiological traits that were evaluated were not measured for the original parental generations, so it is difficult to establish whether the observed differences in metabolic rates and anaerobic capacity occurred in response to selection. Nevertheless, the relationship that was identified between these physiological traits and differential vulnerability to angling has implications for the daily activities of fish in terms of energy acquisition and swimming performance. As a result, selection against high vulnerability to angling risks altering natural populations of recreationally exploited fish in physiological and behavioral terms, potentially affecting their performance of certain behaviours, based on these physiological parameters (Uusi-Heikkilä et al. 2008). Further research is needed on the question of whether the differences in metabolic rates have ecological consequences and affect fitness of fish selected for high and low vulnerability to angling. If this link is made, recreational fishing-induced evolution might have repercussions for wild fish stocks.

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Spatial distribution of Atlantic salmon (*Salmo salar*) breeders: among- and within-river variation and predicted consequences for offspring habitat availability

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Abstract: The spatial distribution of breeders within populations may have important implications for offspring habitat availability in species where mobility of early life stages is restricted. Here we address this issue using time series of spawner distributions from eight Norwegian Atlantic salmon (*Salmo salar*) populations. Whereas spawners distribute themselves uniformly along the length of the rivers in some populations, others show a heavily skewed distribution. Linear mixed models identified pronounced and temporally consistent among-population differences in spawner distributions. Using a model of limited juvenile dispersal from nests following emergence, we show that the observed spawner distributions are predicted to result in significant proportions of rivers being inaccessible for young of the year during early life stages, and the magnitude of this effect differs among populations (e.g., ranging from 27% to 59% for dispersal distance of 250 m). Thus, assuming population regulation during early but not later juvenile stages, consistent differences in spawner distributions among populations such as those observed here may translate into differences in productivity (i.e., carrying capacity) as well as egg densities required for populations to reach their spawning targets.

Résumé : La répartition spatiale de la reproduction au sein des populations peut avoir de sérieuses conséquences sur la disponibilité des habitats pour les rejetons, si la mobilité des premiers stades de vie de l'espèce est limitée. Nous examinons le problème à l'aide de séries chronologiques de la répartition des reproducteurs dans huit populations de saumons atlantiques (*Salmo salar*) de Norvège. Alors que les reproducteurs se répartissent de façon uniforme le long du cours des rivières dans certaines populations, d'autres populations ont une répartition fortement asymétrique. Des modèles linéaires de mélange révèlent des différences marquées et constantes dans le temps entre les populations dans la répartition des reproducteurs. Un modèle de dispersion limitée des jeunes au sortir des nids après leur émergence prédit que les répartitions observées des reproducteurs ont pour conséquence de rendre de grandes parties des rivières inaccessibles aux jeunes de l'année durant leurs premiers stades de vie; l'importance de cet effet varie d'une population à une autre (par ex., allant de 27 % à 59 % pour une distance de dispersion de 250 m). Si on présume que la régulation de la population se fait durant les premiers stades juvéniles mais non durant les stades suivants, des différences constantes de répartition des reproducteurs entre les populations, comme celles signalée ici, peuvent entraîner des différences de productivité (c'est-à-dire, de stock limite) et de densités d'œufs nécessaires pour que les populations atteignent leurs cibles de fraie.

[Traduit par la Rédaction]

Introduction

For many aquatic organisms the degree of mobility changes throughout ontogeny. For example, many marine macroinvertebrates have relatively sedentary preadult and adult stages, whereas their pelagic eggs and larvae can disperse over large distances before settling. Conversely, fish species with demersal eggs and larvae may have limited mobility during these stages, but as for many other organisms they may experience a pronounced increase in mobility with increasing body size (Roff 1991; Clobert 2001). The spatial distribution of breeding adults, which may be free to move over large areas, then determines the spatial distribution of the resulting offspring. A number of mechanisms may shape the spatial distribution of breeders. Physical requirements to breeding or mating habitat accompanied by a

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nonrandom distribution of suitable areas may constrain the distribution of reproduction. Social interactions and interactions with other species may also be important. Both sexually selected reproductive behaviour such as lekking (e.g., Windle and Rose 2007) and antipredator related behaviour (e.g., schooling during reproduction; Axelsen et al. 2000) may produce distinct spatial patterns in the distribution of breeding.

Irrespective of the underlying mechanism, one particularly interesting aspect of spatial patterns in breeding is that it may dictate the density experienced and the amount of habitat accessible for offspring in organisms with limited early life mobility (Ohgushi 1995; Price et al. 1995; Kocik and Ferreri 1998). Deviations from a uniform distribution (or in the case of habitat heterogeneity, an ideal free distribution) may increase the strength of density-dependent mortality and are likely to be important for the population dynamics through effects on the carrying capacity and total recruitment of the population (Einum et al. 2008*a*). Yet, despite its potential importance, information on spatial patterns is rarely included explicitly in studies of population dynamics for the type of organisms where it is likely to be of importance. Usually, this can be ascribed to a lack of data of sufficient spatial resolution, forcing individuals within a given population to be treated as a group that experiences the same environmental conditions (i.e., the mean-field approximation, e.g., Hiebeler 2000). In fact, for most organisms, even qualitative predictions are lacking regarding the role of spatial distributions of breeders in shaping patterns of population dynamics among populations and within populations over time.

Here we examine the potential importance of spatial breeding patterns using time series of spawner distributions from eight Atlantic salmon (*Salmo salar*) populations along the coast of western Norway. Atlantic salmon spawn in rivers where juveniles live for 1–8 years before migrating to the sea. Salmonid females show active choice with regard to the physical habitat for breeding (Armstrong et al. 2003), and sites of breeding may therefore be aggregated within rivers. Returning adult females build discrete nests in which they deposit anywhere from hundreds to thousands of eggs. Thus, any aggregation of breeding will result in pronounced spatial heterogeneity in the distribution of eggs within populations. Because of limited dispersal of juveniles from nests (Beall et al. 1994; Webb et al. 2001; Einum and Nislow 2005), such heterogeneity in the distribution of eggs can influence the subsequent spatial distribution and growth of juveniles during their first summer, both over small spatial scales (tens of metres) in experimental situations (Einum et al. 2008*b*) as well as over larger spatial scales (hundreds of metres) in natural populations (Foldvik et al. 2010). Furthermore, the restricted mobility of offspring following emergence from nests (median dispersal distance < 100 m; Einum and Nislow 2005) can cause intense competition and local density-dependent mortality (Einum and Nislow 2005; Einum et al. 2008*b*). Thus, rather than responding to high local density by dispersing and utilizing unused areas, it appears that individuals may die on-site, perhaps because of starvation (Kennedy et al. 2008), and (or) that individuals attempt to disperse but are unable to do so successfully during the early stages when predation from older fish may be strong (García De Leániz et al. 2000; Henderson and Letcher 2003). As juveniles become older, they respond to high local density by increasing dispersal, consistent with expectations based on increasing mobility with body size (Einum et al. 2006). When incorporating these processes into population models they predict dramatic effects of spawner distributions on population dynamics (e.g., stage-specific patterns of density dependence, adult population size, maximum sustainable yield; Greene and Beechie 2004; Einum et al. 2008*a*). Thus, in the present study we test whether the spatial distribution of spawners varies consistently among populations and years, and hence whether this can contribute to variation in population dynamics. Furthermore, using these data we also model the proportion of the total habitat within the river accessible to juveniles as a function of maximum dispersal distance. The results are discussed in relation to river-specific spawning targets and stock–recruitment relationships.

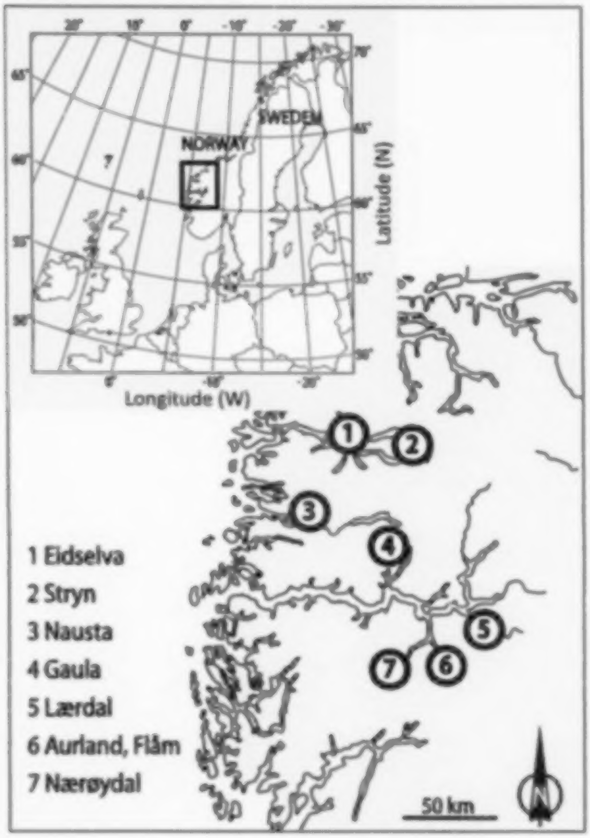
Material and methods

Spawner distributions

We use time series of yearly variation in the distribution of spawning Atlantic salmon from eight rivers along the coast of western Norway (Fig. 1). The distribution data were collected by either snorkeling observations (Orell and Erkinaro 2007) or direct observations from the river bank (Table 1). All observations where done at the time close to or in the start of the spawning period. The observed distribution of spawners at this time will coincide closely with the distribution of actual spawning (Finstad et al. 2005). For the snorkeling counts, diver teams drifted downstream side by side 2–15 m apart, with the distance depending on the width of the river and the water clarity. The number of spawning salmon was registered in sections varying in length (Table 1), depending on physical conditions in the river and the number of salmon observed. Observations from the riverbed were conducted by one or two persons walking along the river during low flow conditions. Here, the rivers were divided into equal sections (50 m long), and the number of observed spawners in each section was registered. Both methods provide minimum estimates on the number of spawners, but because of the high visibility in these rivers (drainage is mainly from mountainous areas resulting in a low input of dissolved organic carbon to the watershed), observations are likely to be independent from local habitat conditions and the spatial patterns accordingly unbiased.

To enable comparisons among rivers, we first calculated the absolute distance from the end of the stretch accessible to Atlantic salmon to the centre of all sections containing spawners in all rivers. We then standardized the position of each observed fish by transforming this distance into a proportion of the total length of river accessible, giving position data ranging from 0 (upstream migration barrier) to 1 (river outlet). For each year and river, the spatial distribution was described by 10 quantiles of the standardized position of the observed spawners (i.e., the standardized position containing cumulative 10% intervals of total spawner counts). The standardized positions for the different quantiles were then used both for visualization and for analyses of the among- and within-river variation in spawner distributions. We

Fig. 1. Position of Norwegian rivers where the spatial distribution of spawning Atlantic salmon was recorded. The neighboring Rivers Aurland and Flåm are indicated by the same point (6).



tested for both river and year effects (nested within rivers) on the distribution of spawning salmon by modeling the standardized position of each *k*th 10 quantile as a function of *k* using linear models. Models with different random effect structures were compared using Akaike's information criterion (AIC) and likelihood ratio tests, based on restricted maximum likelihood (Zuur et al. 2009). In addition to the fixed effect of standardized position, the alternative models included (*i*) no random effect, (*ii*) river as random factor, and (*iii*) river as random factor and an interaction between the fixed (standardized position) and the random (river) factor. The first model assumes a similar spatial distribution in all rivers, the second model allows for variation in intercepts among rivers, and the third one allows for variation in both slope and intercept among rivers. Thus, for the third model, the error term in the model represents among-year, within-river variation in the position of the different quantiles. To quantify the amount of variation in the position of the different quantiles that were caused by random factors, we used variance component analyses, separating variation explained by random terms (Crawley 2007, p. 638). Visual inspection of residuals from the best model did not reveal heteroscedastisity or deviations from normality. The analyses were carried out using the function "lmer" in the "lme4" package (Bates et al. 2008) in R 2.6.0 for Windows (R Development Core Team 2008).

Modeling accessible juvenile habitat

To model the proportion of the total habitat within the river accessible to juveniles as a function of maximum dispersal distance, we used the subset of the data where observations on a 50 m resolution were available (i.e., five rivers, Table 1). The starting point for the model is the presence or absence of spawners within each 50 m section in a given river for a given year. We then assume that if spawners are present within a 50 m section, these include at least one female and spawning occurs at the centre of the section. Finally, we calculate the proportion of the total river habitat that is accessible for resulting juveniles during the first few weeks (Fig. 2), when competition is expected to be severe and survival highly density dependent (Einum and Nislow 2005). Since dispersal limits are unknown and may vary among rivers, we modeled available habitat under different maximum downstream dispersal distance scenarios (Fig. 2). Although some upstream dispersal from nests may occur, this is expected to be limited both with respect to frequency and distance during the initial stage (García De Leániz et al. 2000), which is when competition and local density-dependent mortality is intense (Einum and Nislow 2005) and hence when the issue of habitat availability may be most important. Downstream dispersal has been observed to occur up to 1 km downstream of nests throughout the first summer (Crisp 1995; Webb et al. 2001), but this appears to be rare, and utilization can therefore be expected to be low for the majority of habitat within such a long distance. Furthermore, long-distance dispersal is likely even less common during the first few weeks after emergence from nests, and Einum and Nislow (2005) reported a median absolute dispersal distance of 41 m (range 0–884 m) 1 month after emergence. We therefore varied maximum dispersal distance from zero to 500 m downstream. Variation in dispersal distance among rivers is unknown, but these limits should at least be applicable to a range of Atlantic populations. Because we implicitly assume in our model that all habitat within a given maximum dispersal distance is equally accessible, our predictions in terms of the proportion of the total river habitat that cannot be utilized for a given dispersal distance by juveniles are likely highly conservative.

Results

Spawner distributions

The mean (across years) distributions varied considerably among rivers, ranging from heavily skewed to almost uniform (Fig. 3). Most populations had a skewed distribution, with the highest frequency of spawners often found in the uppermost parts of the river. Visual examination of the 10 quantiles suggested some temporal consistency in spatial patterns among rivers (Fig. 4). Furthermore, there appeared to be some variation in the temporal consistency among rivers, with some populations (e.g., Lærdal) showing minor differences in the spatial distribution among years, whereas others (e.g., Nærøydal) varied considerably (Fig. 4). This was also confirmed in the comparison of alternative linear

Table 1. Study rivers in Norway, position of outlets, and various data collected.

River	River outlet	Length	Years surface	Years snorkeling	Section length	Spawner counts	Years
Aurland	60°54′N, 7°11′E	9.8	1966–1993	2000–2005	350 (185)	65 (43)	33
Eidselva	61°54′N, 5°59′E	10	—	1999, 2001	774 (465)	228 (227)	2
Flåm	60°52′N, 7°08′E	4.7	1988–1994, 1998	2001–2005	368 (230)	54 (40)	8
Gaula	63°21′N, 10°14′E	12.7	—	2000–2002	699 (296)	258 (60)	2
Lærdal	61°06′N, 7°28′E	24.8	1979–1982, 1984–1994	—	—	603 (281)	14
Nausta	61°31′N, 5°44′E	10	—	2000–2003	447 (195)	278 (166)	3
Nærøydal	60°53′N, 6°51′E	11.1	1989, 1991, 1992, 1994, 1998–2005	—	—	70 (43)	12
Stryn	61°54′N, 6°43′E	5.5	1990, 2000, 2002, 2003	—	—	98 (33)	4

Note: Length, length of river accessible to anadromous fish (km); Years surface, years with observations of spawner distribution using observations from river bank; Years snorkeling, years with snorkeling surveys, Section length, mean section length (± standard deviation, SD) of observations in snorkel surveys; Spawner counts, mean number of spawners counted by snorkeling and surface observations each year (±SD); Years, total number of years included in the study, snorkeling and surface observations combined.

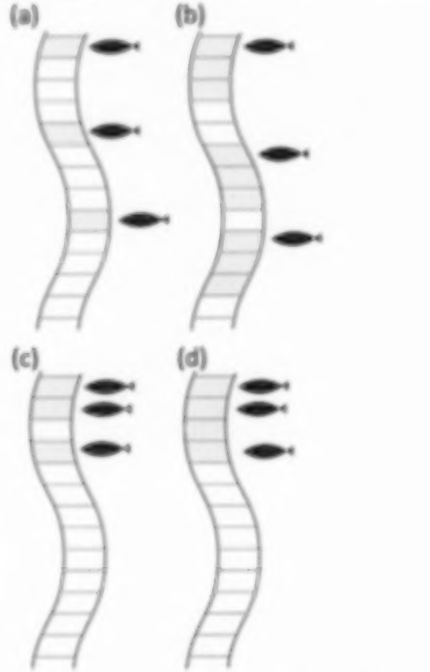


Fig. 2. Schematic illustration of the approach for modeling proportion of river habitat available for juvenile Atlantic salmon as a function of spawner distribution and juvenile dispersal distance. Two scenarios for maximum dispersal distance of juveniles (*a* and *c*: 50 m; *b* and *d*: 150 m) and two scenarios for spawner distribution (*a* and *b*: even; *c* and *d*: more clumped) are given. River habitat accessible for juveniles under the four scenarios is indicated by shaded sections.

mixed models. The full model, which included quantile number as a fixed factor and river as a random factor as well as interactions between these, fitted significantly better than the model without the interaction ($p < 0.001$), and had the lowest AIC value (full model, –1429; model including river as a random factor without interactions, –1349; model with no random effect, –831). For the best model, most of the variation in quantile positions was accounted for by the differences among rivers (89.7%), and only 10.3% of the variance (residual variance) was not explained by the full model and hence could be attributed to variation among years within rivers.

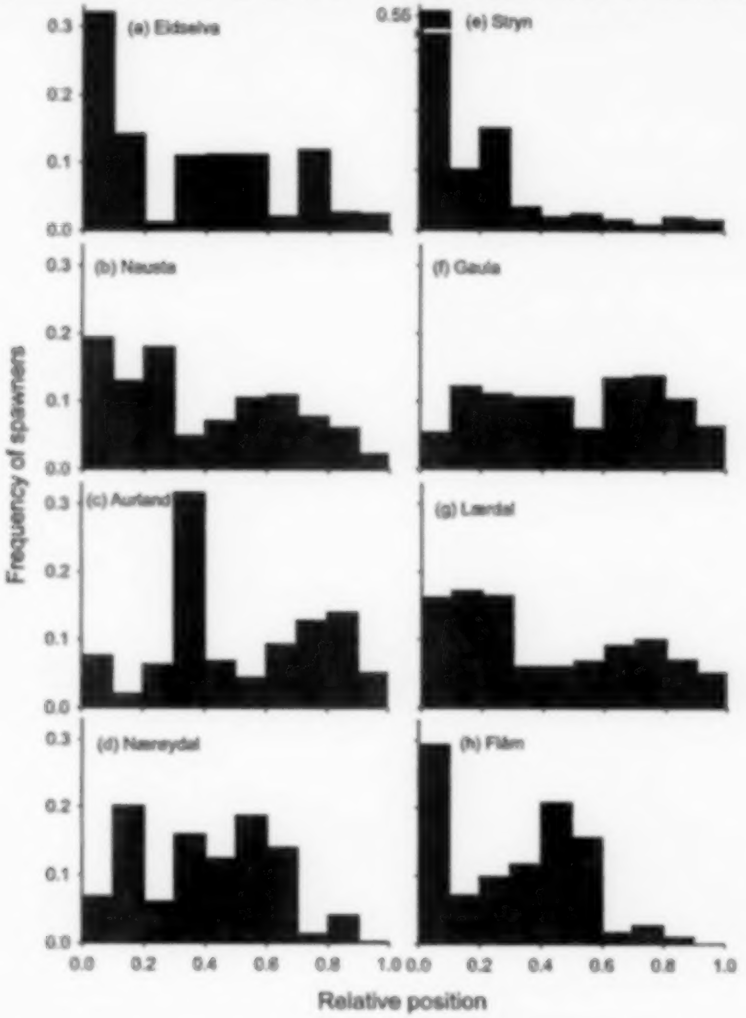
Modeling accessible habitat

Given the observed patterns in the spatial distributions of spawners, the proportion of the river habitat accessible to juveniles also varied considerably both among rivers and within rivers among year (Fig. 5). Intuitively, the proportion of accessible river habitat increased with increasing dispersal distance. This increase was in most cases asymptotic, because of increasing degree of spatial overlap in accessible habitat for juveniles from more than one spawning location. However, even for the largest maximum dispersal distance modelled (500 m), large proportions of rivers were inaccessible for juveniles, with the average varying between 42% and 11% of the total area for the different rivers. For a more realistic dispersal distance (250 m), juveniles were on average only able to utilize between 41% and 73% of the total habitat for the different rivers (Fig. 5*f*). Because of the within-river variation in spawning distributions across years, there was also considerable temporal variation in the proportion of river accessible. For the River Aurland, accessible river habitat given a 250 m dispersal distance varied between 10% and 76% (Fig. 5*b*). There was, however, pronounced differences among rivers in the magnitude of this effect, with River Lærdal, being one of the temporally most stable rivers, varying only between 63% and 78% among years (Fig. 5*e*).

Discussion

Although the effects of spatial patterns of breeding on offspring performance and population dynamics of salmonid species has gained increased interest (Einum and Nislow 2005; Einum et al. 2008*a*; 2008*b*), analyses of spatial breeding patterns from natural populations have been lacking. In the present study, we demonstrate differences in Atlantic salmon spawner distributions among rivers that are consistent over time. Whereas some populations have a rather even distribution of spawners along the length of their rivers, others show a more spatially patchy distribution. Furthermore, we show that the observed spawner distributions are predicted to result in significant proportions of rivers being inaccessible to juveniles following emergence from

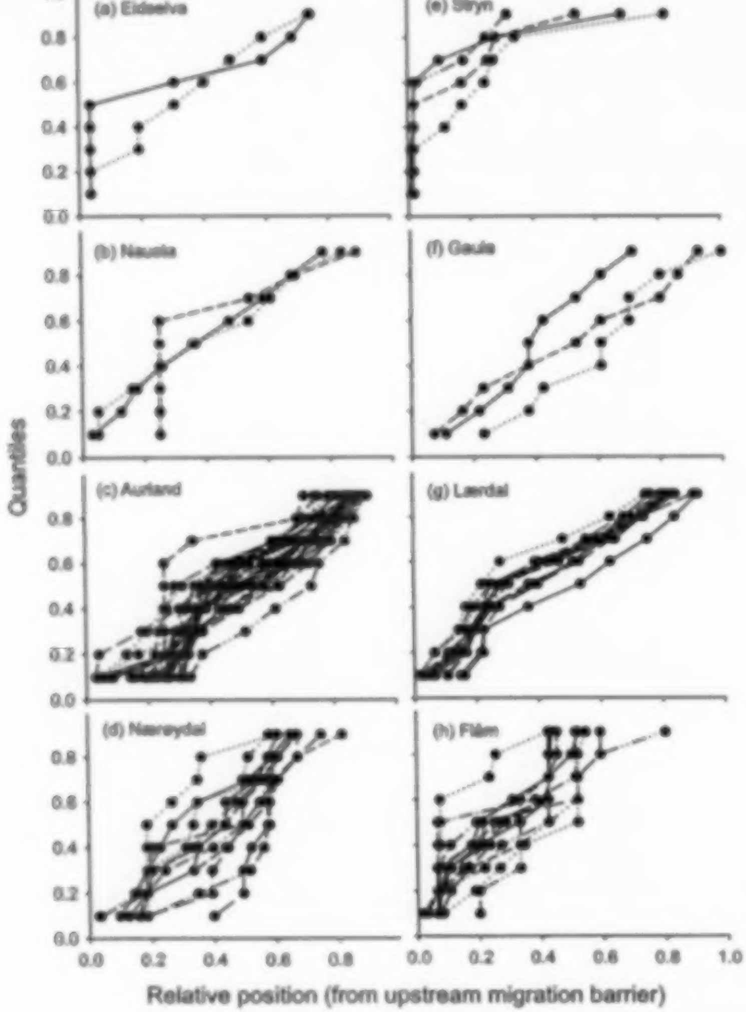
Fig. 3. Distribution of Atlantic salmon spawners (averaged over years) in the study rivers. Position is given as distance standardized relative to the total length of the accessible river. Zero denotes adult Atlantic salmon migration barriers, and 1 is the outlet of the river.



nests. Thus, breeding behaviour in terms of spatial decisions is likely to be important for the population dynamics of this species. One of the main predictions arising from the spatially explicit model of Einum et al. (2008*a*) is that, given population regulation during early but not later juvenile stages, rivers with a uniform spatial spawner distribution are predicted to have a higher carrying capacity (i.e., higher smolt and adult production at equilibrium) than those with a more clumped distribution. Thus, consistent differences in spatial distributions among populations such as those observed here may contribute to differences in productivity.

Among-population differences in spawning distribution are likely related to the specific habitat requirements of spawning female Atlantic salmon (Armstrong et al. 2003). Geomorphologic properties within each watershed together with flow patterns will govern the channel morphology on local scales and accordingly determine the spatial variation in spawning habitat suitability (Kocik and Ferreri 1998; Montgomery et al. 1999; Isaak et al. 2007) and hence distribution of spawners. In addition, restrictions on upstream migration caused by migration barriers may reduce the accessibility of suitable sites (Thorstad et al. 2008). Although the among-river variation in spawning distributions was found to be pronounced, there was also residual variation in the linear mixed model, which represented within-river variation among years. A wide range of factors may be responsible for such variation. For example, it may be related to annual differences in physical habitat features. Particularly, migration obstacles, such as waterfalls, may hinder spawning fish to reach areas upstream in the river, and the severity of such obstacles may be highly dependent on water flow or temperature, which varies among years (Thorstad et al. 2008). However, some of the largest among-year variation in spawning distributions in our study was found within the Rivers Aurland and Flåm, both having a relatively flat gradient and no obvious migration barriers.

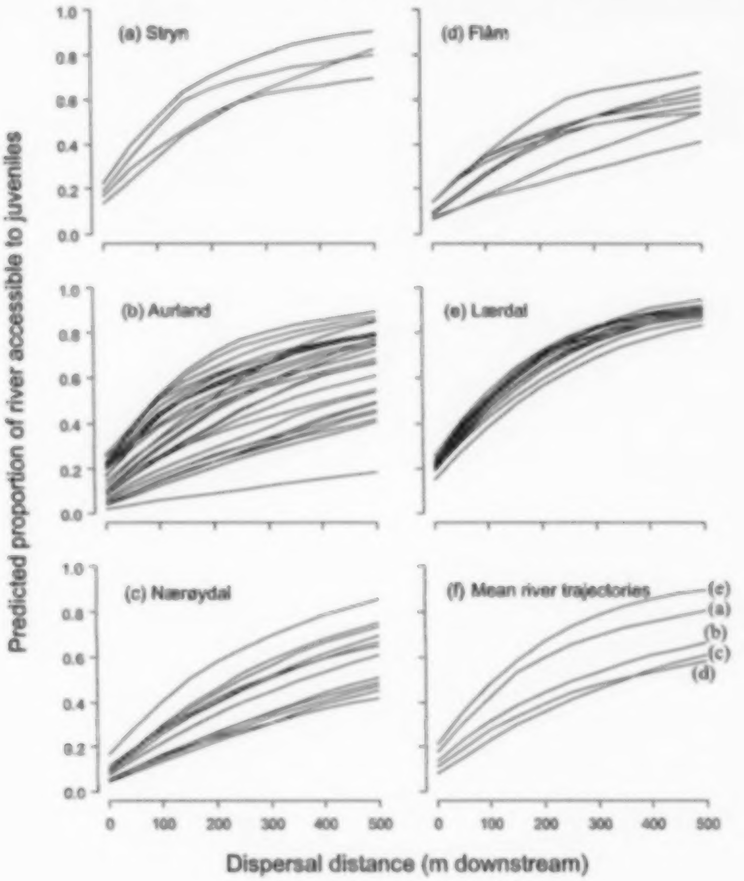
Fig. 4. Yearly 10 quantiles for the number of Atlantic salmon spawners plotted against relative position (as given in Fig. 3) for the study rivers. For each year and river, the standardized positions containing cumulative 10% intervals of total spawner counts are shown.



Thus, other processes may be just as likely responsible for among-year variation in distributions. Annual differences in the spatial patterns of harvesting or predation within rivers could be one such alternative source to this variation. In addition, local homing combined with spatial asynchrony in population dynamics or density-dependent behavioural interactions (competition, attraction) leading to deviations from ideal free distributions would produce such variation (Purchase and Hutchings 2008). Although our understanding of such annual variation in the spatial distribution of spawners within rivers is limited, it seems clear that it may produce pronounced variation in the resulting spatial distribution of juveniles as well as in the proportion of river habitat being accessible following emergence from nests; hence, it may also contribute to temporal variation in smolt and adult production.

If the observed patterns of spawner distributions among and within rivers translate into effects on population dynamics as predicted by models (Einum et al. 2008*a*), incorporating such knowledge into management appears prudent. The management of Atlantic salmon is to an increasing degree being based on the identification of spawning targets (ST), representing the number of spawners (and by extension eggs) required for different populations to satisfy some desired recruitment strength (e.g., Ó Maoiléidigh et al. 2004; Chaput et al. 1998; Hindar et al. 2007). Because identification of STs is based on empirical stock–recruitment relationships, and such data are absent for most populations, one of the main challenges for management is to transfer knowledge from data-rich to data-poor rivers. One solution to this, being applied for most populations across Canada and the USA, is to use a common egg density requirement (or apply different requirements in different types of habitats, such as fluvial and lacustrine habitats) and then calculate the ST for rivers based on their total area (Baum 1995;

Fig. 5. Proportion of the river habitat being accessible to juvenile Atlantic salmon modeled as a function of dispersal distance for year-specific spawning distributions. Only study rivers in which spawning distribution data had been collected at 50 m scales (*a–e*) are included. Bottom right panel (*f*) shows mean values for the different rivers, with different rivers being indicated with letters corresponding to panels (*a–e*).



O'Connell and Dempson 1995). Alternatively, among-river geographical patterns in egg density requirements may be modelled from rivers where stock–recruitment data are available, enabling predictions for rivers without such information (e.g., along latitudinal gradients of European populations; Prévost et al. 2003), a method in use for Irish salmon stocks (Anonymous 2007). A common feature for these approaches is that they ignore the spatial structure of populations within rivers. The present study demonstrates how the distribution of spawners as well as the availability of habitat for emerging juveniles is a river-specific characteristic. Based on this, rivers are predicted to differ in their carrying capacity and egg density requirement, even with everything else being equal (Einum et al. 2008*a*). Attempts at adjusting egg density requirements on an individual river level in the absence of stock–recruitment data has been done for a large number of Norwegian salmon populations by using available information on productivity, such that rivers that are shown to have a high smolt or adult production (relative to their area) get assigned a higher egg density requirement (Hindar et al. 2007). Given little variation in density-independent mortality among populations, such an approach will implicitly include effects of spawning distributions. However, use of productivity measures may introduce bias if large differences in density-independent mortality from the egg to the recruit stage exist among populations (populations exposed to particular anthropogenic or natural environmental challenges will be assessed to require a lower egg density). Thus, in the absence of population-specific stock–recruitment relationships, including data on the spatial distribution of spawners and (or) spawning habitat in an explicit manner may be used as an additional tool when developing Atlantic salmon spawning targets.

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Coldwater fish oxythermal habitat in Minnesota lakes: influence of total phosphorus, July air temperature, and relative depth

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Abstract: An empirical model was developed that describes the influence of lake productivity, climate, and morphometry on coldwater fish oxythermal habitat. An oxythermal habitat variable called temperature at $3\ \mathrm{mg \cdot L^{-1}}$ of dissolved oxygen (T_{DO3}) was developed by interpolating the water temperature at a benchmark oxygen concentration ($3\ \mathrm{mg \cdot L^{-1}}$) from a temperature–oxygen profile. Coldwater habitat was most available in the least productive lakes (total $P < 25\ \mu\mathrm{g \cdot L^{-1}}$) with the greatest relative depths (geometry ratios $< 2\ \mathrm{m^{-0.5}}$) and where mean July air temperatures were less than 17 °C. Species response curves were developed from values of T_{DO3} measured during the greatest period of oxythermal stress in late summer ($\max T_{\mathrm{DO3}}$). Lake trout was present in lakes with the lowest values of $\max T_{\mathrm{DO3}}$, while cisco was present in lakes with the highest and broadest range of $\max T_{\mathrm{DO3}}$. Projections for a scenario where climate warming (+4 °C in mean July air temperature) was accompanied by eutrophication (doubling of total P) indicated that coldwater fish oxythermal habitat would be devastated in a subset of lakes typical for Minnesota. Protecting deep, unproductive lakes from eutrophication will be a necessary management strategy to ensure that coldwater fish persist in at least some Minnesota lakes after climate warming.

Résumé : Nous mettons au point un modèle empirique qui décrit l'effet de la productivité lacustre, du climat et de la morphométrie sur l'habitat oxythermique des poissons d'eau froide. En interpolant la température de l'eau à une concentration repère d'oxygène ($3\ \mathrm{mg \cdot L^{-1}}$) dans un profil de température–oxygène, nous obtenons une variable de l'habitat oxythermique, soit la température à $3\ \mathrm{mg \cdot L^{-1}}$ d'oxygène dissous (T_{DO3}). L'habitat d'eau froide se retrouve le plus couramment dans les lacs les moins productifs (P total $< 25\ \mu\mathrm{g \cdot L^{-1}}$) avec les profondeurs relatives les plus grandes (rapports géométriques $< 2\ \mathrm{m^{-0.5}}$) et une température moyenne de l'air en juillet de moins de 17 °C. Nous avons mis au point des courbes de réaction des espèces à partir des valeurs de T_{DO3} mesurées durant la période de stress thermique maximal en fin d'été (T_{DO3} maximum). Les touladis se retrouvent dans les lacs qui ont les valeurs les plus basses de T_{DO3} maximum, alors que les ciscos vivent dans les lacs avec les étendues des valeurs de T_{DO3} maximum les plus élevées et les plus larges. Des projections selon un scénario dans lequel le réchauffement du climat (+4 °C de température moyenne de l'air en juillet) est accompagné d'une eutrophisation (dédoublement du P total) indiquent que l'habitat oxythermique des poissons d'eau froide serait dévasté dans un sous-ensemble de lacs typiques du Minnesota. Il sera nécessaire d'adopter une stratégie de gestion pour protéger les lacs profonds et peu productifs de l'eutrophisation afin d'assurer que les poissons d'eau froide survivent au moins dans certains lacs du Minnesota après le réchauffement climatique.

[Traduit par la Rédaction]

Introduction

Coldwater fish in north temperate lakes are especially vulnerable to the effects of eutrophication and climate change (Evans et al. 1996; Magnuson et al. 1997; Stefan et al. 2001). During the summer stratification period, the physiological requirement of coldwater stenotherms for cold, well-oxygenated water is usually met within hypolimnia in north temperate, dimictic lakes. However, the high hypolimnetic oxygen concentrations that characterize suitable habitat for coldwater fish during summer can be reduced to lethal levels by increased rates of organic material deposition and decay brought on by eutrophication (Nürnberg 1995). Extended periods of summer stratification from climate warming should further reduce hypolimnetic oxygen concentrations in productive, stratified lakes (De Stasio et al. 1996; Stefan et al. 1996). Lake depth also affects hypolimnetic oxygen concentrations and coldwater fish habitat (Molot et al. 1992; Fang et al. 2004). Deep lakes with large hypolimnia maintain the highest concentrations of dissolved oxygen during stratification (Cornett and Rigler 1979; Charlton

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Table 1. Attributes of the 1623 lakes located throughout Minnesota used in the development of the generalized additive model of coldwater habitat.

Parameter	Units	Minimum	First quartile	Median	Third quartile	Maximum
Area	ha	0.4	40.0	95.1	252.6	89 392.7
Maximum depth	m	0.7	6.4	10.9	17.3	64.9
Geometry ratio	$m^{-0.5}$	0.47	1.90	2.89	4.73	42.87
Total phosphorus	$\mu g \cdot L^{-1}$	4	18.3	29.2	62.6	722
Mean July air temperature	°C	16.2	20.1	22	22.4	23

1980). Teasing apart the relative influences of productivity, climate, and lake morphometry on hypolimnetic oxygen should advance our understanding of the relative effects of eutrophication and climate warming on coldwater fish resources.

Empirical models of coldwater fish habitat have proven useful for the management of species such as lake trout (*Salvelinus namaycush*) in boreal forest lakes (Ryan and Marshall 1994; Steedman and Kushneriuk 2000; Dillon et al. 2003). These oxythermal habitat models generally involve measuring the volume or thickness enclosed by an upper temperature bound and a lower dissolved oxygen concentration bound. Boundaries delineated by values representing either optimal thermal habitat (Dillon et al. 2003) or nonlethal–usable habitat (MacLean et al.1990; Ryan and Marshall 1994) have commonly been used. Dillon et al. (2003) inserted a lower oxygen concentration bound into a common hypolimnetic oxygen profile model (Molot et al. 1992; Clark et al. 2002), set an upper temperature bound in a temperature model, and then combined the models to examine the effects of lake productivity on optimal lake trout habitat. Ryan and Marshall (1994) developed an empirical model of hypolimnetic oxygen concentrations that defined a niche boundary for lake trout based on lake depth (mean depth) and primary productivity (total phosphorus (P), chlorophyll *a*, and Secchi depth). They explored the effect of climate change by increasing the duration of summer stratification in their model. In addition, thermal habitat volume has been shown to be correlated with yields of lake trout (Christie and Regier 1988; Marshall 1996; Siesennop 2000) and lake whitefish (*Coregonus clupeaformis*) (Christie and Regier 1988).

Minnesota, USA, is in a geographical position that spans the productive agricultural soils of a prairie ecoregion, through a transition ecoregion of hardwood forests, and then into the shallow, unproductive soils of the boreal forest – Precambrian Shield. Lake productivities range from highly eutrophic (>500 $\mu g \cdot L^{-1}$ of total P) to oligotrophic (<10 $\mu g \cdot L^{-1}$ of total P). Mean July air temperatures range from 23 °C in the prairies of southwestern Minnesota to 16 °C in the boreal forests of the northeastern part of the state. Four indigenous species of coldwater fish are relatively common in Minnesota: cisco (*Coregonus artedi*) (known to exist in 648 lakes in Minnesota), lake whitefish (155 lakes), burbot (*Lota lota*) (233 lakes), and lake trout (124 lakes). The several thousand lakes in the state that do not support coldwater taxa provide a substantial contrast for quantifying oxythermal habitat. In addition, a broad range of lake productivities and climates allows for a more general analysis of factors affecting coldwater fish habitat than previous models specific to boreal lake trout (Ryan and Marshall 1994; Steedman and Kushneriuk 2000; Dillon et al. 2003).

The goal of our study was to develop an empirical model that describes the effects of lake productivity, climate, and morphometry on coldwater fish habitat in Minnesota lakes using an index of oxythermal conditions. This analysis included a broad range of lake types and coldwater species (cisco, lake whitefish, burbot, and lake trout). Indices of productivity and climate were considered to be environmental forcings that are partially human-dependent, and a morphometric index was a fixed covariate for each lake. Such a coldwater habitat model essentially represents a fundamental, *n*-dimensional physiological niche (Hutchinson 1957) that describes the oxythermal environment where coldwater species can survive and reproduce. One challenge for developing a general model was to formulate a variable that quantified oxythermal habitat across species that have different requirements for cold, oxygenated water. Temperature at a benchmark oxygen concentration of 3 $mg \cdot L^{-1}$ was selected as a general oxythermal habitat variable (see Materials and methods). Presence and absence of the four coldwater taxa in Minnesota lakes were compared along an environmental gradient of the variable to define species-specific, oxythermal niches (Guisan and Zimmermann 2000). The empirical model was then used to explore the relative effects of eutrophication and climate change on the oxythermal niche of each coldwater species.

Materials and methods

Field methods

Temperature and oxygen profiles from 1623 widely distributed lakes (Table 1) were measured by the Minnesota Department of Natural Resources (MDNR) and Minnesota Pollution Control Agency (MPCA) at 0.30 or 1 m intervals in the deepest part of lakes using electronic meters with polargraphic membranes. Epilimnetic water samples were collected using either a 2 m long, 32 mm diameter polyvinyl chloride (PVC) pipe integrated sampler or surface grab samples. Chemical analyses of total P were performed by the Minnesota Department of Agriculture, Department of Health, or at MPCA-approved laboratories. MPCA data were retrieved from the US Environmental Protection Agency (USEPA) STORET database, and MDNR data were retrieved from internal databases (http://www.pca.state.mn.us/index.php/water/water-home.html). Only profiles and water chemistry samples taken during the period when lakes were consistently stratified (May through September) were used in the analysis. A total of 9521 temperature and oxygen profiles and 26 507 total P measurements for the years 1993 through 2005 were available.

Potential outliers were identified by examining extreme values (usually obvious data entry errors deemed highly unusual for the data set). In addition, a parameter that measured the relative influence of each observation on a lake mean was developed, $(|x_i - \bar{x}|/\bar{x})/n$, where x_i is the individual observation, $\bar{x}$ is the lake mean, and n is the number of samples for the lake). Observations with large relative influences were examined for obvious data entry errors.

The presence or absence of four coldwater fishes was determined from 2235 MDNR standard gillnetting assessments on 997 lakes from 1993 through 2005 (the 997 lakes were a subset of the 1623 lakes with temperature and oxygen profile data). The standard gillnets, consisting of 75 m of graded mesh multifilament material (15 m panels of 19, 25, 38, 51, and 64 mm bar-measure mesh × 2 m deep), were set overnight during the months of June, July, and August. Gillnets (n = 2 to 15 for each assessment, where n was based on lake size) were placed on the lake bottom at or above the thermocline, generally targeting cool-water species such as walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). Because important hypolimnetic habitats were sampled poorly with these standard gillnets, abundance (catch per effort) data obtained for coldwater species were of limited value (catch per effort was likely correlated poorly with abundance). Presence or absence data for each coldwater fish taxa were assumed to be more reliable than catch per effort data and were used for the analysis. For lake trout, only lakes with native populations (data from MDNR files) were included in the analysis (lake trout introductions have been more common than lake whitefish, burbot, and cisco introductions in Minnesota).

Single oxythermal habitat variable development

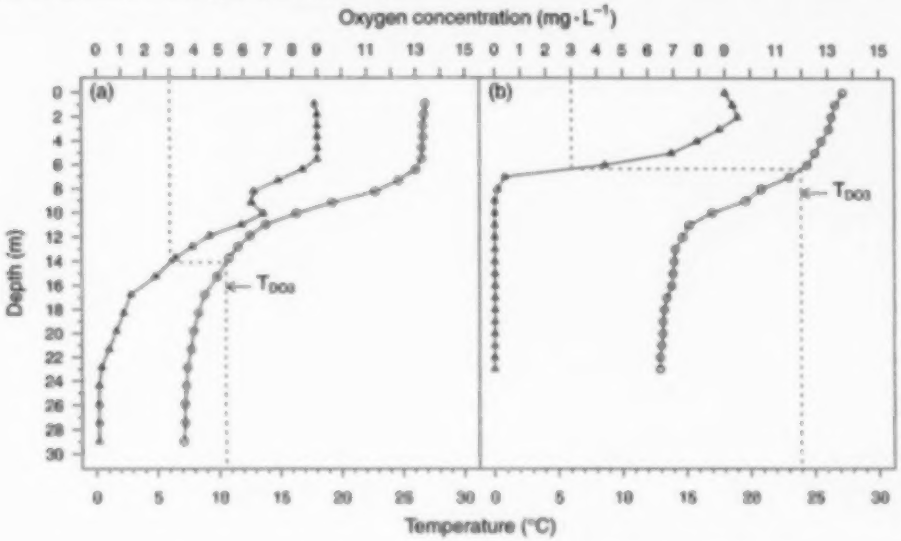
Since oxythermal habitat envelopes commonly used in coldwater fish niche modeling define species-specific temperature and oxygen concentration boundaries (e.g., Ryan and Marshall 1994; Dillon et al. 2003), a more general measure of the availability of cold, oxygenated water was developed that would allow for direct comparisons across taxa and simplify modeling the effects of productivity, morphometry, and climate on oxythermal habitat. A generalized oxythermal habitat variable called temperature at 3 $mg \cdot L^{-1}$ of dissolved oxygen (T_{DO3}) was derived by interpolating the temperature of water at a benchmark oxygen concentration (3 $mg \cdot L^{-1}$) from a temperature–oxygen profile during the summer stratification period. In lakes where oxygen concentrations and water temperatures decrease monotonically below the thermocline, T_{DO3} represents the coldest water where oxygen concentrations remain at or above the benchmark concentration. In lakes with profiles that are nonmonotonic (e.g., metalimnetic oxygen maxima or minima), where more than one value of T_{DO3} is possible, the coldest value was used. Although identification of a single oxygen concentration that has similar physiological consequences for all coldwater taxa was impossible, selecting a benchmark concentration that represents an undesirable level for all species was useful for a developing the generalized oxythermal habitat variable. Several benchmark concentrations (2, 3, 4, and 5 $mg \cdot L^{-1}$) were considered and all were highly correlated. However, 3 $mg \cdot L^{-1}$ is an oxygen concentration that is probably lethal or nearly so for many coldwater species (Frey 1955; US Environmental Protection Agency 1986; Evans 2007) and represented a suitable benchmark for a presence–absence niche model. Lower values of T_{DO3} indicate better oxythermal habitat for coldwater fish (i.e., there should often be a wide range of temperatures available in the hypolimnion with sufficient oxygen concentrations). Higher values of T_{DO3} indicate poorer oxythermal habitat for coldwater fish, containing less cold water with sufficient oxygen. Very high values of T_{DO3} indicate hypolimnia that are anoxic or unstratified lakes lacking cold water. Examples of lakes with a low and high value of T_{DO3} are illustrated (Fig. 1). With this single variable, the varying oxythermal requirements of different coldwater fishes can then be described and compared.

Coldwater habitat model development

A coldwater habitat model was developed that empirically describes the relationship between cold, oxygenated water and two environmental forcing factors (productivity and climate) and a morphometry covariate. Total P is a primary nutrient limiting lake productivity in north temperate lakes (Schindler 1977) and is a common focus of efforts directed at reducing the effects of cultural eutrophication (Carpenter et al. 1998). Mean July air temperature was the primary climate forcing factor used in the analysis. Mean July air temperature is an integrated measure of the effects of summer climate on aquatic ecosystems (Larocque et al. 2001) and is a common factor that helps explain fish distributions in lakes (MacCrimmon and Marshall 1968; Barbour and Brown 1974; Shuter et al. 1980). Mean July air temperature has also proven useful for projecting the effects of climate change on fish distributions and community relationships (Keleher and Rahel 1996; Jackson and Mandrak 2002). Mean July and August temperatures have also been correlated with longer durations of stratification (King et al. 1997). Mean July air temperature for each lake was obtained from the WorldClim database (Hijmans et al. 2005), which spatially interpolated temperatures (from 1950 to 2000) from meteorological station and elevation data using smoothing splines. Spatial resolution of the WorldClim data was 30 arc seconds (commonly referred to as 1 km resolution), while temperature resolution was 0.1 °C. The WorldClim value for mean July air temperature at the location nearest the geographical center of each lake was used.

Incorporating morphometry as a covariate was important because of its important effect on hypolimnetic size and coldwater fish habitat (Cornett and Rigler 1979; Charlton 1980). Deeper lakes inherently have thicker hypolimnia and greater potential for coldwater fish habitat. Because mixing depth is a often function of lake size (especially lakes >500 ha; Fee et al. 1996), measures of depth relative to lake size are important for modeling hypolimnetic thermal habitat. Geometry ratio ($A_0^{0.25}/z_{max}$, where A_0 is surface area (m^2) and z_{max} is maximum depth (m)) has been successfully used to classify stratification status of the lakes (Hondzo and Stefan 1996) and is a measure of relative depth (i.e., it incorporates lake size). Fee et al. (1996) used a similar transformation (fourth root of surface area; $A_0^{0.25}$) and measured a linear relationship with mixing depth. Nürnberg (1995) established that a related depth variable ($\bar{z}/A_0^{0.5}$,

Fig. 1. Examples of T_{DO3} (temperature at 3 mg·L^{-1} dissolved oxygen) determined from temperature (circles) and oxygen (triangles) profiles in (*a*) a lake with good coldwater oxythermal habitat (T_{DO3} = 10.6 °C; Rose Lake, 46.675°N, 95.740°W, A_0 = 481 ha, z_{max} = 42 m, total P = 17.0 µg·L^{-1}, 3 August 2006) and (*b*) a lake with poor coldwater oxythermal habitat (T_{DO3} = 23.9 °C; Little Pine Lake, 46.634°N, 95.557°W, A_0 = 797 ha, z_{max} = 19 m, total P = 29.8 µg·L^{-1}, 25 July 2006).



where $\bar{z}$ = mean depth) was significantly correlated with duration of hypolimnetic anoxia. As a relative depth variable, geometry ratio uses commonly available data on lake size (surface area) and maximum depth and has the additional property of being useful for classifying stratification status.

A generalized additive model (GAM; Hastie and Tibshirani 1990) was used to relate the response variable (T_{DO3}) to predictor variables of total P, July air temperature, and geometry ratio. The mgcv (multiple generalized cross validation) package in the statistical program R (R Development Core Team 2003) was used for the calculation of the GAM. The mgcv implementation fitted a series of penalized regression splines as smoothing functions for each predictor variable and suggested degrees of freedom for smooth terms by minimizing the generalized cross validation score (Wood 2006). Smooth terms were manually adjusted when a more parsimonious model (fewer degrees of freedom) was desired. A Gaussian family, with an identity link function, was used for the GAM.

An initial coldwater habitat GAM was generated using oxygen and temperature profiles from all warm months (May through September), with numeric day of year as an additional predictor variable. The period of greatest oxythermal stress for coldwater fish (30-day period with the highest values of T_{DO3}) was identified using the model. Additional GAMs were generated from subsets of the data representing stratified and unstratified lakes (also for all warm months). These sorted GAMs allowed for comparison of the relative effects of lake productivity and climate by stratification status.

Coldwater niche definition

Presence or absence of the four coldwater species was modeled using a species response curve along an environmental gradient approach (Guisan and Zimmermann 2000; Oksanen and Minchin 2002). The environmental gradient was the availability of cold, oxygenated water in late summer represented by values of T_{DO3} calculated from profiles measured during the 30-day period of highest oxythermal stress (maxT_{DO3}). GAMs were developed for each species, with probability of occurrence as the response variable and maxT_{DO3} as the predictor variable. A logistic link function, appropriate for binomial presence–absence models (Oksanen and Minchin 2002), was used for the species response GAMs. GAMs are especially useful for modeling species–environment relationships where responses are commonly asymmetric and nonlinear (Guisan et al. 2002).

Heegaard's (2002) central and outer borders were used as measures of niche breadth within each species response curve. Niche breadth measures are useful for quantifying the range of a species response to an environmental variable: some species are tightly "bound" to a narrow range of an environmental variable (such as oxythermal habitat), while others have a wider tolerance. Heegaard's (2002) central and outer borders placed benchmarks on the species response curves that facilitated comparison across species. Specifically, they were the points where the response values (probability of occurrence) were equal to ± maximum response × exp(−½) for central borders and ± maximum response × exp(−2) for outer borders. Central and outer borders are nonparametric analogs to niche breadth measures of parametric species response functions (ter Braak and Looman 1986) and are well suited for asymmetric responses generated by GAMs (Heegaard 2002). Central borders were assumed to bracket the core range of coldwater habitat required for each species to survive and thrive. Outer borders were assumed to represent the entire range of oxythermal habitat for each species (Heegaard 2002).

Table 2. Generalized additive model (GAM) estimated degrees of freedom (df) and significance of smooth terms (*F* statistic and approximate *P* value) of predictors (geometry ratio, total P, mean July air temperature, and day of year) on the response variable (temperature at 3 $mg \cdot L^{-1}$ dissolved oxygen) for models with profiles from all lakes (n = 9521), stratified lakes (n = 6399), and unstratified lakes (n = 3122).

Smooth term	Estimated df	*F*	*P*
All lakes			
Geometry ratio	8.64	526.9	<0.001
Total phosphorus	8.80	58.2	<0.001
Mean July air temperature	2.31	434.0	<0.001
Day of year	8.29	971.8	<0.001
Stratified lakes			
Geometry ratio	2.75	739.2	<0.001
Total phosphorus	7.89	60.2	<0.001
Mean July air temperature	2.67	300.4	<0.001
Day of year	8.28	617.9	<0.001
Unstratified lakes			
Geometry ratio	2.91	48.7	<0.001
Total phosphorus	7.84	3.1	0.001
Mean July air temperature	1.00	500.9	<0.001
Day of year	8.28	685.1	<0.001

Model projections of future climate warming and eutrophication

The effects of climate warming and eutrophication on coldwater oxythermal habitat was projected for specific lakes with the empirical coldwater oxythermal model. These projections were straightforward because of the use of July air temperature and total P as environmental forcing variables. Under a climate warming scenario, mean July air temperature was projected to increase by 4.0 °C — the approximate midpoint of summer temperature increases projected for the US Midwest by the year 2099 from of a number of general circulation models reported by Wuebbles and Hayhoe (2004). Total P concentrations were assumed to double under the eutrophication scenario — an increase observed in Minnesota lakes with watersheds heavily disturbed by agriculture and urbanization (Ramstack et al. 2004). MaxT_{DO3} was estimated under the eutrophication and climate warming scenarios for 246 stratified lakes using the empirical model. These lakes were selected because they represented a typical cross-section of Minnesota lakes and numerous temperature–oxygen profiles measured during the period of greatest oxythermal stress were available.

Results

Coldwater habitat model

Total P, July air temperature, relative depth, and day of year all significantly affected coldwater habitat (Table 2), and the general model for all lakes explained 69% of the deviance in T_{DO3} (adjusted r^2 = 0.689, n = 9521). Relative depth and day of year had large effects on coldwater habitat. Values of T_{DO3} were lowest in lakes with the greatest relative depths (geometry ratios < 2 $m^{-0.5}$) and higher in relatively shallow lakes (Fig. 2). Geometry ratios larger than 4 $m^{-0.5}$ had little effect on coldwater habitat. A geometry ratio of 4 $m^{-0.5}$ effectively marked the transition between stratified and unstratified lakes. Low values of T_{DO3} were more frequent in hypolimnia of stratified lakes than in unstratified (isothermal) lakes. The highest values of T_{DO3} were found in late summer (late July and early August). T_{DO3} was low in spring, when hypolimnia were oxygenated, and in fall, when epilimnia cooled. T_{DO3} peaked on 4 August.

Total P and July air temperature, the two environmental forcing variables, each had a significant influence on coldwater habitat. T_{DO3} was lowest in the least productive lakes (total P concentrations < 20 $\mu g \cdot L^{-1}$). Productive lakes (total P concentrations > 40 $\mu g \cdot L^{-1}$) had the highest values of T_{DO3}. The effect of July air temperature on coldwater fish habitat was nearly linear — T_{DO3} was greater for lakes with higher mean July air temperatures.

Coldwater habitat models sorted by stratification status

Influences of geometry ratio and total P on coldwater habitat differed between stratified and unstratified lakes (Fig. 3, Table 2). Geometry ratio strongly affected coldwater habitat in the stratified lakes, and the shape of the response was similar to the general GAM truncated at a geometry ratio of 4 $m^{-0.5}$. However, geometry ratio had only a small influence on T_{DO3} in unstratified lakes. Total P in the stratified lakes had a threshold type effect on coldwater habitat, similar to the general GAM. T_{DO3} decreased sharply when total P was less than 25 $\mu g \cdot L^{-1}$. However, total P had little effect on T_{DO3} in unstratified lakes.

The period of greatest oxythermal stress for coldwater fish differed by stratification status. Stress occurred earlier in unstratified lakes (Fig. 3). Maximum values of T_{DO3} occurred on 27 July in unstratified lakes vs. 11 August in stratified lakes. The 30-day period of greatest oxythermal stress went from 13 July through 12 August for unstratified lakes and 28 July through 27 August for stratified lakes. The

Fig. 2. Generalized additive model (GAM) estimated responses of oxythermal habitat (temperature at 3 mg· L^{-1} dissolved oxygen, T_{DO3}) to (*a*) relative depth (geometry ratio), (*b*) productivity (total P), (*c*) climate (mean July air temperature), and (*d*) day of year. The *y* axis of each plot is on a scale where zero (dashed line) equals the mean effect on T_{DO3} of each variable and shaded area represents ±2 standard errors (error associated with the response, not the distribution of individual response, which are narrow because of the large sample size).

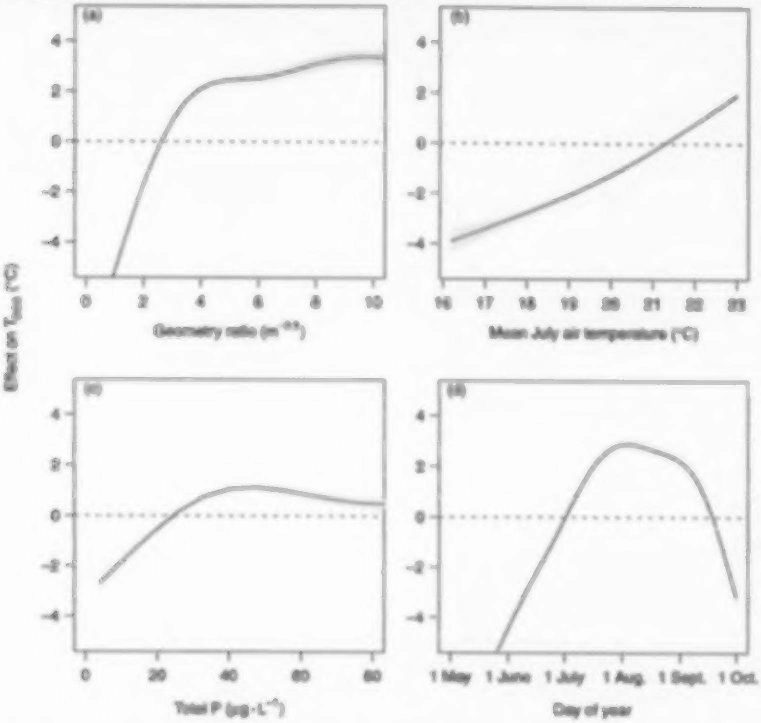


Fig. 3. Generalized additive model (GAM) estimated responses of oxythermal habitat (temperature at 3 mg·L^{-1} dissolved oxygen, T_{DO3}) to relative depth (geometry ratio), productivity (total P), climate (mean July air temperature), and day of year for stratified (*a*) and unstratified (*b*) lakes. The *y* axis of each plot is on a scale where zero (dashed line) equals the mean effect on T_{DO3} of each variable and shaded area represents ±2 standard errors. Vertical lines bracket the 30 days of highest oxythermal stress. Note the *x* axis scale is different for the geometry ratio plots.

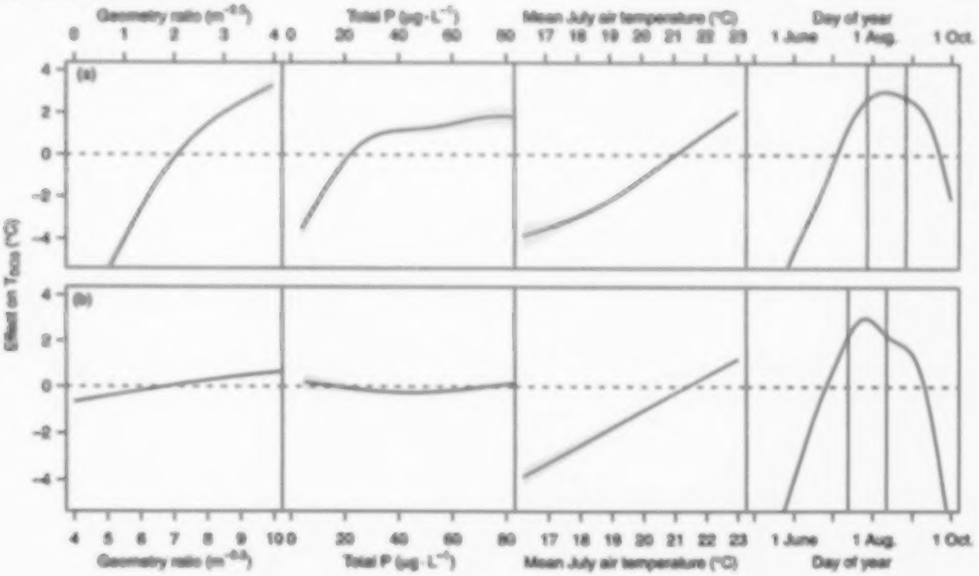
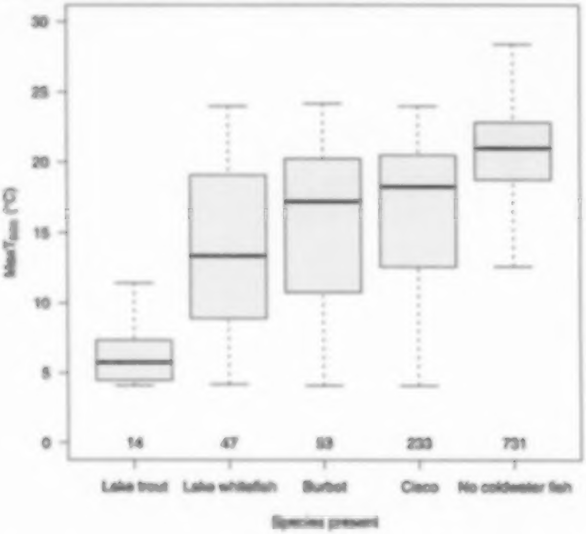


Fig. 4. Box plots of maxT_{DO3} (temperature at 3 mg·L^{-1} dissolved oxygen interpolated from profiles measured during the periods of greatest oxythermal stress; 27 July through 26 August for stratified lakes and 13 July through 12 August for unstratified lakes) measured in 997 Minnesota lakes where four coldwater species were captured vs. lakes lacking those species. Bold horizontal lines represent medians, boxes represent interquartile ranges (25th–75th percentiles), and extended dotted lines represent 1.5 × interquartile ranges. Number of lakes is presented below respective box plots (more than one species were captured in some lakes).



models explained 65% of the deviance in T_{DO3} for the stratified lakes and 68% for the unstratified lakes.

Coldwater niche properties

Distributions of maxT_{DO3} for lakes in which the four coldwater species were present or absent illustrated differences in oxythermal habitats (Fig. 4). Among lakes containing at least one coldwater species, median values of maxT_{DO3} were lowest for lakes with lake trout (5.7 °C) and highest for lakes with cisco (18.2 °C), with values intermediate for lakes with lake whitefish (13.4 °C) and burbot (17.2 °C). Lakes where lake trout were present had the narrowest interquartile range of maxT_{DO3} (1.5 °C). Lake whitefish, burbot, and cisco were captured from lakes that had wider interquartile ranges of maxT_{DO3} (10.2, 9.4, and 7.9 °C, respectively). Of the 265 lakes where coldwater species were present, median values of maxT_{DO3} were 17.4 °C for the 234 stratified lakes and 21.0 °C for the 31 unstratified lakes. Lake whitefish, burbot, and cisco were the only taxa captured in unstratified lakes. Values of maxT_{DO3} were considerably higher in the 731 lakes where no coldwater species were captured (19.6 °C for the 395 stratified lakes and 22.4 °C for the 336 unstratified lakes).

Species response curves further illustrated the different coldwater habitat requirements by defining the oxythermal niche for each of the four coldwater taxa (Fig. 5). Lake trout were associated with the lowest values of maxT_{DO3} and were rarely captured in lakes with values of maxT_{DO3} > 10.0 °C. Cisco were captured in lakes with the highest values maxT_{DO3}. The highest probability of cisco occurrence was at a maxT_{DO3} of 9.0 °C, while maximum occurrence of the other species occurred at 4.0 °C. Response curves of lake whitefish and burbot were intermediate to lake trout and cisco, with the highest probabilities of occurrence at the lowest values of maxT_{DO3}. Lake trout were also associated with the coldest central niche borders and cisco with the warmest (Table 3). Central borders for burbot and lake whitefish were intermediate to lake trout and cisco. Outer borders showed similar species differences (Table 3). All central and outer borders started at the coldest values of maxT_{DO3} available (4.0 °C).

Fig. 5. Generalized additive model (GAM) fitted logistic regressions of probability of occurrence of four species of coldwater fish based on gillnet catches in 997 Minnesota lakes from 1993 to 2005 as a function of maxT_{DO3} (temperature at 3 mg·L^{-1} dissolved oxygen interpolated from profiles measured during the periods of greatest oxythermal stress; 27 July through 26 August for stratified lakes and 13 July through 12 August for unstratified lakes).

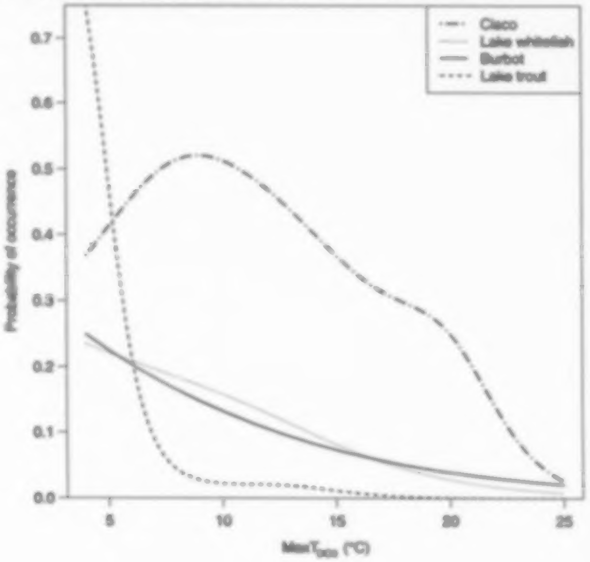


Table 3. Central and outer borders (Heegaard 2002) of the species response curves (Fig. 5) of maxT_{DO3} (temperature at 3 mg·L^{-1} dissolved oxygen interpolated from profiles measured during the periods of greatest oxythermal stress; 27 July through 26 August for stratified lakes and 13 July through 12 August for unstratified lakes).

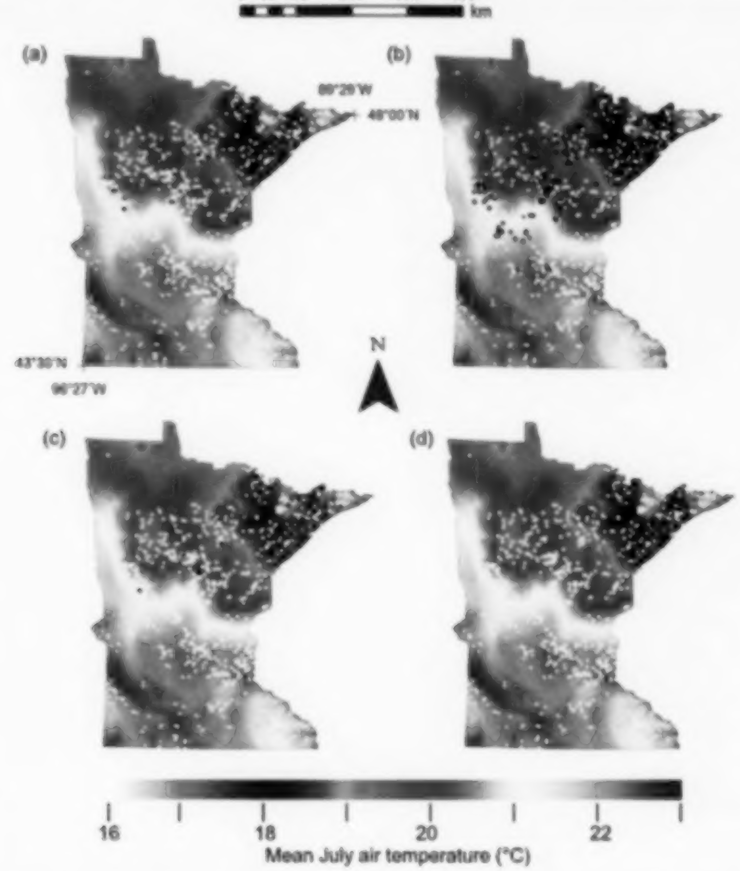
Species	Maximum occurrence (°C)	Central border range (°C)	Outer border range (°C)
Lake trout	4.0	4.0–5.1	4.0–6.8
Burbot	4.0	4.0–8.8	4.0–21.1
Lake whitefish	4.0	4.0–11.1	4.0–19.5
Cisco	9.0	4.0–16.9	4.0–23.4

Note: Temperatures below 4 °C were not recorded

Geographic distributions

Based on lakes in which coldwater fish were captured with standard MDNR gillnets (1993–2005), cisco was the

Fig. 6. Geographic distribution of 997 Minnesota lakes that were sampled with standard gillnets from 1993 to 2005. Black dots represent presence and white dots represent absence of four species of coldwater fish: (*a*) burbot, (*b*) cisco, (*c*) lake whitefish, and (*d*) lake trout.



most widely distributed coldwater fish, captured in 233 lakes, primarily in the northern and central portions of the state (Fig. 6). Cisco was the only coldwater fish captured from areas with mean July air temperatures greater than 21 °C. The 32 lakes that contained coldwater taxa other than cisco were confined to the Precambrian Shield in the northeastern corner of the state. Lake trout were captured in the fewest lakes (14), mostly located on the Precambrian Shield near the Ontario, Canada, border. Lake whitefish (47 lakes) and burbot (53 lakes) had distributions intermediate to lake trout and cisco and occurred primarily in north–central and northeastern portions of the state.

Model projections of future climate warming and eutrophication

Histograms of predicted maxT_{DO3} under eutrophication (doubling of total P) and climate warming (increased mean July temperature of 4.0 °C) scenarios on the subset of 246 stratified lakes are presented (Fig. 7). Projected climate warming increased values of predicted maxT_{DO3} more than the eutrophication scenario (a greater shift to the right in the histograms). The combined climate warming and eutrophication scenario resulted in the highest values of predicted maxT_{DO3}. The number of lakes within central and outer niche borders also shifted more under climate warming than eutrophication (Table 4). Under the scenario where the climate warming was accompanied by eutrophication, oxythermal conditions in none of the lakes would remain within central borders for lake trout and burbot, and only 8% (3 of 40 lakes) for lake whitefish would remain within central borders. Thirty-eight lakes (45%) would be projected to remain within the central borders for cisco.

Discussion

Coldwater oxythermal habitat was significantly affected by total P, July air temperatures, and relative lake depth. However, how these factors affected coldwater fish habitat differed between stratified and unstratified lakes (differences also observed by Fang et al. 2004). Total P and relative depth had strong effects on oxythermal habitat in stratified lakes, but not in unstratified lakes. Unstratified lakes lack a hypolimnia and oxythermal habitat was more affected by surface warming and subsequent mixing of the entire water column. The direct effects of surface warming on coldwater habitat for salmonids in unstratified lakes were also observed by Lehtonen (1998) and Malmquist et al. (2009). Also, the period of greatest oxythermal stress in stratified lakes was later than in unstratified lakes because hypolimnetic oxygen depletion continues even after epilimnetic cooling begins in late summer. However, climate had similar effects in both stratified and unstratified lakes with nearly linear responses of coldwater habitat to July air temperatures. Apparently, duration of stratification affects subsequent oxygen depletion (and thus T_{DO3}) in a linear fashion in stratified lakes, while effects of mean July air temperatures on lake temperatures (and thus T_{DO3}) are also linear in unstratified lakes.

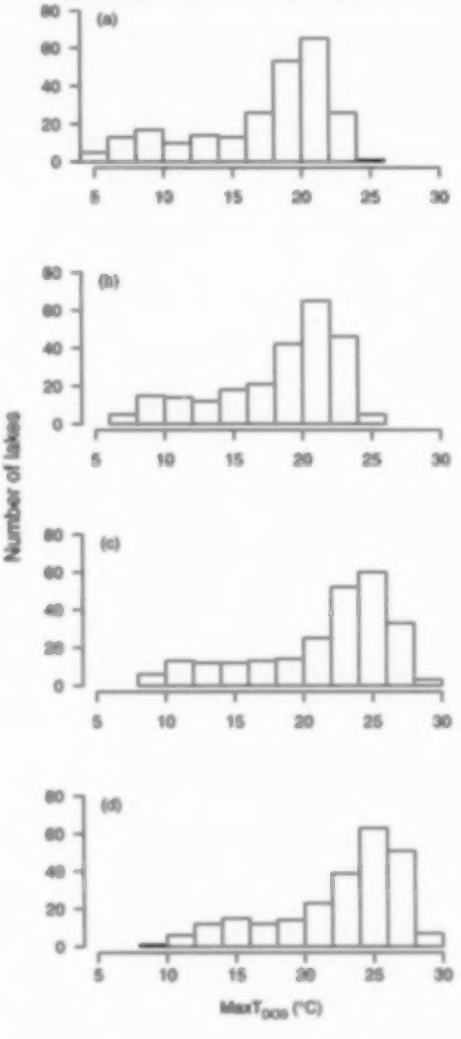
Temperature at 3 mg·L^{-1} DO was a measure of coldwater habitat that effectively described the oxythermal niches of four species of fish in Minnesota. Heegaard's (2002) central and outer borders of maxT_{DO3} were useful for quantitatively comparing the species-specific oxythermal niches. Calculated using simple linear interpolations of temperature and oxygen profiles, T_{DO3} should be useful for fisheries managers. Measurements of temperature and oxygen profiles during the period of greatest oxythermal stress in late summer provided for a useful application of this oxythermal variable as a diagnostic tool. Profiles measured during the first 2 weeks in August would provide a standard measure of the quality of oxythermal habitat during the period of greatest oxythermal stress for both stratified and unstratified lakes in Minnesota.

The GAMs captured important nonlinearities in the oxythermal habitat and species-specific niche models. For example, the sharp break at 25 µg·L^{-1} of total P in the response of oxythermal habitat to lake productivity in stratified lakes has potential for developing effective targets for protecting and restoring coldwater fish habitat (i.e., stratified lakes with total P concentrations that exceed 25 µg·L^{-1} likely offer little coldwater fish habitat in the hypolimnion). The sharp break at a geometry ratio of 4.0 m$^{-0.5}$ in the response of oxythermal habitat to lake morphometry presented a convenient method for separating the effects of stratification status on coldwater fish habitat in Minnesota lakes. Correspondingly, the nonlinear species responses to oxythermal habitat were also effectively illustrated with the generalized additive niche models (Guisan et al. 2002).

Of the four coldwater species, lake trout clearly had the most extreme requirement for cold, oxygenated water. Lake trout were present only in deep, oligotrophic lakes in the region of Minnesota with the coolest July air temperatures. Values of maxT_{DO3} were considerably lower in lakes with lake trout than in lakes with other species, and the geographical range of lake trout was the most restricted. The coldwater stenothermal nature of lake trout is well documented, and several authors have synthesized studies of lake trout thermal ecology (Christie and Regier 1988; MacLean et al. 1990; Evans 2007). The requirements for cold, oxygenated water by the four coldwater taxa present in Minnesota followed the same general order observed by Marshall and Ryan (1987) in Ontario lakes.

Oxythermal niche benchmarks for coldwater fish calculated in this study are related to measures of temperature and oxygen requirements documented by other authors. For example, oxygenated water within the optimal lake trout temperature range of 8–12 °C estimated by Christie and Regier (1988) is available in lakes that have values of maxT_{DO3} less than the upper outer border of 6.8 °C. MacLean et al.'s (1990) "usable" habitat envelope of 15.5 °C and 4.0 mg·L^{-1} is contained within the outer borders for lake trout. The optimal habitat envelope of 10 °C and 6.0 mg·L^{-1} described by Martin and Olver (1980) and Dillon et al. (2003) is probably more related to the upper central border (5.1 °C at 3 mg·L^{-1} DO), which describes the core habitat of the species.

Fig. 7. Histograms of (*a*) current oxythermal habitat conditions habitat (late summer temperature at 3 mg·L^{-1} dissolved oxygen) and projected for scenarios of (*b*) eutrophication (doubling total P concentrations: TP×2), (*c*) climate warming (4 °C increase in mean July air temperature: JulyTemp+4), and (*d*) both stressors (TP×2 and JulyTemp+4) for 246 stratified Minnesota lakes.



The benthic nature of burbot (Carl 1995) and lake whitefish (Vander Zanden and Vadeboncoeur 2002) may contribute to their specific requirement for high quality coldwater habitat. Coldwater fish that require benthic habitat are confined to the profundal zone of north temperate lakes in the

Table 4. Current oxythermal habitat conditions and projected scenarios of eutrophication (doubling total P concentrations: TP×2) and climate warming (4 °C increase in mean July air temperature: JulyTemp+4) for 246 stratified Minnesota lakes.

Scenario	Lake trout	Burbot	Lake whitefish	Cisco	Outside all borders
Lakes within central niche borders					
Current	2	25	40	84	159
TP×2	0	11	31	70	173
JulyTemp+4	0	2	13	49	194
TP×2 and JulyTemp+4	0	0	3	38	205
Lakes within outer niche borders					
Current	11	136	187	237	6
TP×2	2	112	157	231	12
JulyTemp+4	0	68	84	123	120
TP×2 and JulyTemp+4	0	54	70	106	137

Note: Numbers of lakes are categorized by potential oxythermal habitat by four coldwater species, based on their central and outer borders (Heegaard 2002) presented in Table 3.

summer. Because hypolimnetic oxygen concentrations are at a minimum near the deepest parts of a lake, only well-oxygenated hypolimnia provide suitable coldwater habitat. Carl (1995) telemetered burbot in Lake Opeongo (a lake with a well-oxygenated hypolimnion) that rested in deep (mean = 13 m), cold water (mean = 9.0 °C) near the bottom during summer days. Burbot foraged actively at night in water as warm as 20 °C, but mean telemetered temperatures were still a relatively cold 10.5 °C. Burbot have been reported to use temperatures of 10.8–11.4 °C (Ferguson 1958), 9–13 °C (Bruesewitz 1990), and 8–13 °C (Edsall et al. 1993), and a final preferred temperature of 14.2 °C was determined in the laboratory by Hofmann and Fischer (2002). Telemetered lake whitefish in Lake Huron (Madenjian et al. 2006) remained in water colder than 10 °C for much of the year. Preferred temperatures for lake whitefish have been reported as 16.8 °C for age-0 (Edsall 1999), 15.6 °C for age-1 (Edsall 1999), and 12.7 °C for age-2 (Ferguson 1958), and Christie and Regier (1988) estimated an optimal temperature range of 10–14 °C. These reported temperature preferences for burbot and lake whitefish are higher than for lake trout and agree with the intermediate thermal requirements measured in this study.

Cisco were the most eurythermal of the four coldwater species. The upper outer border of 23.4 °C for cisco was the highest of the four coldwater species, and border ranges were considerably wider than for congeneric lake whitefish. Although laboratory thermal physiological measurements made on cisco are few, Edsall and DeSorcie (1999) measured an optimum temperature for growth at 14.5 °C, a final preferendum of 16.5 °C, and an upper incipient lethal temperature of 26 °C for age-0 cisco. They also noted a greater thermal tolerance than in other coregonines and attributed that partly to the ability of age-0 cisco to withstand relatively high temperatures. Jacobson et al. (2008) measured incipient lethal temperatures for adult cisco during summer mortality events of 24 °C. Frey (1955) noted the relatively high thermal tolerance of the cisco at their southern range limit in Indiana and defined a "cisco layer" as the depth strata bounded by 20 °C and 3 mg·L^{-1} of oxygen.

The geographical ranges of all four of these coldwater species extend far to the north of Minnesota (Scott and Crossman 1973), thus, species responses at very cold temperatures and climates were undefined in this study. Indeed, maximum probabilities of occurrence were generally at the lowest measured summer temperatures available in Minnesota. Schlesinger and Regier (1983) concluded that lake whitefish yields were maximized when mean annual air temperatures were −1 °C. However, none of Minnesota has a mean annual air temperature less than 0 °C, which suggests that climate in the state cannot be "too cold" for coldwater fish. (Although species response of cisco was somewhat reduced at the lowest values of maxT_{DO3}, many of the lakes without cisco and with low values of maxT_{DO3} occur in the northeastern part of the state, where rugged terrain formed barriers that may have reduced postglacial colonization opportunities for cisco.) Fish community composition (especially species richness) varies greatly across Minnesota (Schupp 1992), from the simple fish communities of the Precambrian Shield lakes to the species-rich communities of central Minnesota (which contain many warm, cool, and coldwater taxa). How existing fish communities and historical dispersal limitations affect fish distributions, in addition to oxythermal habitat effects, is an interesting question for future research.

The projected increases in maxT_{DO3} from increased temperature and P illustrated the detrimental consequences of eutrophication and climate warming on coldwater fish habitat. Although the climate warming scenario increased maxT_{DO3} more than the eutrophication scenario, when both stressors operated concurrently, coldwater fish habitat was devastated. These results suggest that protecting or improving water quality in relatively deep lakes is a useful climate change adaptation strategy. For example, the model identified a number of lakes that would still provide excellent oxythermal habitat for cisco (58% of the modeled lakes) and for lake whitefish (33% of the modeled lakes) after climate warming, if they were protected from eutrophication. Maintaining water quality in these "refuge" lakes is an adaptation strategy that should ensure some coldwater fish will survive in a climate-warmed Minnesota.

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Larval entrainment in cooling water intakes: spatially explicit models reveal effects on benthic metapopulations and shortcomings of traditional assessments

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Abstract: Spatial management of marine populations typically requires consideration of larval dispersal pathways. When a power plant with a cooling water intake system (CWIS) is present, managers must also account for reductions in larval supply to natural habitats due to larval entrainment in the CWIS. To evaluate the consequences of CWIS entrainment for benthic populations, we coupled a transport model for an idealized coastline to a spatially explicit metapopulation model. CWIS entrainment reduced the probability of dispersal to and from sites near the CWIS. However, the reductions in larval supply due to entrainment generally produced only minor, localized effects on adult population density because of postsettlement density-dependent mortality. Only when population densities were already reduced by other forms of adult or larval mortality did entrainment threaten population persistence. Our simulations suggest that subpopulations several kilometres upstream of CWIS make the greatest contribution to metapopulation persistence by countering the effects of CWIS entrainment, and these locations should be the focus of conservation efforts to enhance larval sources. Finally, we show that traditional statistics used to estimate the demographic effects of CWIS entrainment are generally inaccurate and unreliable because they ignore nonlinearities in population dynamics.

Résumé : La gestion spatiale des populations marines nécessite généralement la prise en compte des voies de dispersion larvaire. Lorsqu'il y a une centrale électrique avec une entrée d'eau de refroidissement (CWIS), les gestionnaires doivent aussi considérer les réductions de l'apport de larves aux habitats naturels à cause de l'entraînement des larves dans la CWIS. Afin d'évaluer les conséquences de l'entraînement dans la CWIS sur les populations benthiques, nous avons couplé un modèle de transport sur un rivage idéal avec un modèle de métapopulation spatialement explicite. L'entraînement dans la CWIS réduit la probabilité de dispersion vers les sites près de la CWIS et à partir d'eux. Cependant, les réductions dans les apports de larves dues à l'entraînement ne produisent généralement que des effets mineurs et localisés sur la densité de la population adulte parce que la mortalité après l'établissement des larves est dépendante de la densité. C'est seulement lorsque les densités de population sont déjà réduites par d'autres formes de mortalité larvaire ou adulte que l'entraînement menace la persistance de la population. Nos simulations indiquent que les sous-populations situées à plusieurs kilometres en amont de la CWIS contribuent le plus à la persistance de la métapopulation en compensant les effets de l'entraînement dans la CWIS; ces sites devraient donc être ciblés par les efforts de conservation afin d'augmenter les sources de larves. Nous montrons enfin que les statistiques traditionnelles utilisées pour estimer les effets démographiques de l'entraînement dans les CWIS sont généralement inexactes et peu fiables car elles ne tiennent pas compte des non-linéarités dans la dynamique des populations.

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Introduction

The implementation of effective marine conservation measures is complicated by the role of larval dispersal in marine population dynamics. Nearly all nearshore, benthic marine organisms possess a two-stage life history. Adults are relatively sedentary, remaining attached to one location or occupying a limited home range for their entire lives. Adults reproduce by spawning eggs and larvae that spend days to months in the water column (Caley et al. 1996). Larvae have relatively limited swimming abilities, especially early in their development, and can be transported long distances by ocean currents (Gawarkiewicz et al. 2007). In order for the population at any coastal location to persist through time, adults that die (or are harvested) must be replaced over time by newly arriving larvae (Armsworth 2002; Hastings and Botsford 2006). Thus, uncertainty about larval dispersal pathways necessarily leads to uncertainty about the persistence of adult populations.

Widespread dispersal during the larval phase may decouple reproductive output at a given location from subsequent larval settlement and demographic replacement at that location. As a consequence, the replacement and persistence of any one local population may depend on the persistence of populations elsewhere in the dispersal network (Hastings and Botsford 2006). Resolving dispersal pathways is thus a critical conservation goal (Cowen et al. 2007). Typically, marine conservation efforts involve scenarios in which dispersal pathways remain constant, but human activities reduce total larval production, either by harvesting large, fecund adults or by impairing the productivity of adult habitat (e.g., Kaplan et al. 2006). An entirely different conservation problem is posed when the dispersal pathways themselves are altered through anthropogenic reduction of larval survival.

Power plants in coastal regions continuously withdraw seawater to recondense superheated steam used in their electricity-generating turbines. These once-through cooling water intake systems (CWIS) are a cost-effective cooling technique, but they are expected to have a large environmental impact on marine populations (California Energy Commission 2005). In addition to the impingement of adult fishes on the mesh screens covering the intake and the thermal disturbance produced when heated seawater is returned to the ocean (two impacts that we do not address in this paper), intakes entrain and kill potentially large numbers of planktonic larvae. Depending on the origin and would-be destination of those larvae, CWIS entrainment could disrupt larval dispersal pathways and thus have a substantial impact on the replacement and persistence of adult populations.

The complexity of nearshore oceanography and the details of spatial replacement and persistence of nearshore populations contrast with the relatively simple quantitative methods currently used to assess CWIS entrainment impacts. Currently used assessment methods fall into two categories (Steinbeck et al. 2007). The adult equivalent loss (AEL) and fecundity hindcasting (FH) methods attempt to estimate the amount of adult mortality that would be equivalent to the larval mortality produced by entrainment (AEL) or estimate how many adults' total reproductive output is represented by the number of entrained larvae (FH) (Steinbeck et al. 2007). These methods require the user to assume that the species of interest has linear population dynamics and that larvae exist in a well-mixed pool, neither of which is likely in a real population of benthic marine organisms. The empirical transport model (ETM) (Boreman et al. 1981) attempts to obtain a more accurate estimate of the fraction of all larvae that are entrained (within some total volume of "source water") by accounting for the heterogeneous distribution of larvae within the source water. This approach, however, does not put the estimate of larval mortality in the context of adult population dynamics. Further, it is not realistic to demarcate the source water for a CWIS along the open coast (as opposed to within a bay or estuary). Given these limitations, it is likely that the traditional approaches are insufficient to accurately project the population-level effects of CWIS entrainment.

To evaluate the general consequences of CWIS entrainment on benthic population dynamics, we developed a transport model for nearshore circulation along an idealized coastline containing a CWIS. We used this transport model to estimate patterns of larval connectivity in a spatially explicit metapopulation model of the coastline. Like Heimbuch et al. (2007*a*, 2007*b*), we relate the effects of entrainment mortality to the overall level of exploitation (i.e., adult mortality) in the metapopulation to compare the relative effects of entrainment and other stressors on demographic persistence. However, our model addresses the case of a generic coastline rather than a specific geographic location. In contrast with most previous models of entrainment effects on marine populations (e.g., Jensen and Hamilton 1982; Summers 1989; Nisbet et al. 1996), we explicitly consider the spatial structure of the population, allowing us to draw conclusions for species in which adults have limited movement and most dispersal is confined to the larval stage (the earlier models are appropriate for well-mixed populations with wide-ranging, pelagic adults). Moreover, an explicit treatment of space is necessary to develop results that can inform the spatial management of resources, such as the placement of marine protected areas (MPAs). While it is generally assumed that the performance of protected areas could be impaired by the presence of CWIS (Roberts et al. 2003; California Department of Fish and Game 2008), no study has yet examined how CWIS or other entraining structures affect the conservation value of nearby locations.

We used our coupled transport–metapopulation model in a strategic, rather than tactical, context. That is, we examined the general effects of CWIS on benthic metapopulations, rather than model a particular study system. The transport model was parameterized using values typical of coastal California, but similar parameter values and results are found in many other coastal environments. Within this framework, we address four questions: (*i*) What is the spatial distribution of entrainment impacts within the metapopulation? (*ii*) How does the distribution of impacts affect spatial management decisions? (*iii*) What is the effect of entrainment on metapopulation persistence? (*iv*) Under what conditions do traditional assessment metrics accurately reflect the population-level effects of entrainment?

Materials and methods

We modeled a benthic population occupying nearshore, shallow, subtidal habitat along a homogenous, one-dimensional stretch of coast consisting of 100 identical cells, each extending 1 km alongshore. For each model cell i, we used a Lagrangian particle tracking model to calculate the dispersal kernel, D, representing the probability of dispersal from i to every other cell. This was done by releasing 10^4 particles (eggs) from a single alongshore cell and examining the spatial distribution of successful settlers (we assume that eggs hatch into larvae at some point after spawning, but there is no functional difference between "eggs" and "larvae" in our model). Each particle was released at a randomly selected location within the 1 km cell and within 10 m of the shoreline. Settlers were defined as those particles that came within 500 m of the coastline at any point during a competency window of T_c days beginning T days after spawning. It was assumed that larvae within 500 m of the shore would find habitat there, be mixed to the shore, or show some active behavior that would allow them to move to nearshore habitats. The CWIS was located near the center of the spatial domain at x = 50.5 km, placing it at the midpoint of the 51st spatial cell. Because CWIS are typically located very near the shoreline, we modeled scenarios in which the CWIS was located at y = 50 m and y = 500 m offshore. The effect of a CWIS on larval particles is simulated by designating a zone of entrainment within which particles are removed from the larval population.

Transport model: Lagrangian particle tracking

We developed a Lagrangian random-walk particle model to simulate larval transport in an idealized coastal environment. The model assumes a straight shoreline at y = 0 m and a zero-flux condition across this boundary. There is no offshore or alongshore boundary in the model (i.e., particles can be tracked beyond the 100 km alongshore domain of the benthic population and return again to the domain). The position of individual particles (larvae), defined by an alongshore coordinate x and a cross-shore coordinate y, is updated each model time-step with displacements resulting from diffusive and advective processes (see Fig. 1 for a schematic of the model, Table 1 for symbols used in the paper, and Largier (2003) for a discussion of what processes contribute to "advection" and "diffusion"). Updates to particle position, Δx and Δy, are performed every time-step (Δt = 120 s) as the sum of advective ($U\Delta t$, $V\Delta t$) and diffusive (L_x, L_y) displacements:

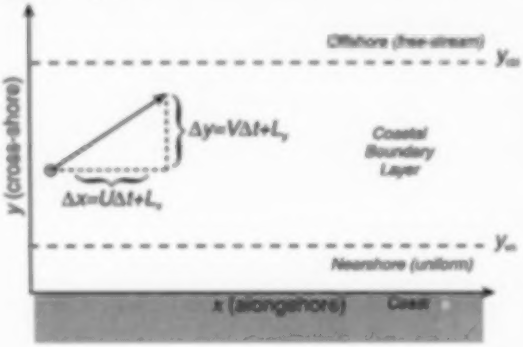
$$(1) \qquad \Delta x = U\Delta t + L_x$$

$$(2) \qquad L_x = [q]_{-1}^{1}\sqrt{6K_x\Delta t}$$

$$(3) \qquad \Delta y = V\Delta t + L_y$$

$$(4) \qquad L_y = \left.\frac{\mathrm{d}K_y}{\mathrm{d}y}\right|_{y(t)}\Delta t + [q]_{-1}^{1}\sqrt{6K_{y^*}\Delta t}$$

Fig. 1. Schematic diagram of the transport model, including the components of movement of a particle (open circle) that is being transported in the direction indicated by the arrow. Gray shading indicates land (y < 0).



where U and V are advection velocities in alongshore and cross-shore directions, respectively; K_x and K_y are eddy diffusivities in alongshore and cross-shore directions, respectively; and $[q]_{-1}^{1}$ is a random number in the interval [–1,1] (Sanchez-Arcilla et al. 1998). Equation 4, the expression for cross-shore diffusive displacement, uses the value of K_{y^*} at position y^*

$$(5) \qquad y^* = y(t) + \frac{1}{2}\cdot\left.\frac{\mathrm{d}K_y}{\mathrm{d}y}\right|_{y(t)}\Delta t$$

which is the expected position of the particle halfway through the time-step. This acts as a correction term, as needed when there is a gradient in diffusivity (Hunter et al. 1993; Visser 1997; Spagnol et al. 2002). This correction term is not needed for alongshore eq. 2 because K_x is homogeneous (zero gradient) in the direction of flow variability ($\mathrm{d}K_x/\mathrm{d}x = 0$). The cross-shore mean velocity V was assumed to be zero everywhere for the time scales of interest here (several days or longer). Only higher-frequency cross-shore flows are found nearshore because the shoreline boundary precludes any cross-shore flow at y = 0. While larvae may effect a mean transport in any direction because of direct swimming or vertical migrations correlated with reversing cross-shore flows, we do not account for these effects here.

Because most CWIS draw water from intakes at the shoreline or very close to shore, entrainment patterns are sensitive to the nature of nearshore circulation. Further, for many nearshore populations, all larvae begin their lives within this zone and must return here to settle. The detailed features of nearshore flow (beyond the surf zone, but within a few kilometres of the shoreline) are poorly understood, but mean and variance in velocity are typically less than in the "free-stream" flow further offshore (Lentz and Winant 1986; Lentz et al. 1999; Noble and Xu 2004). Because of this limited knowledge and the difficulty of resolving nearshore flows, most dispersal modeling frameworks have either completely excluded the nearshore from the model domain or assumed that flows are uniform in the nearshore (e.g., Siegel et al. 2003). However, growing empirical evidence suggests that many larvae spend the entire planktonic period nearshore (Morgan et al. 2009; Shanks and Shearman

Table 1. List of symbols used in the paper.

Symbol	Definition
Particle tracking model	
D_{ij}	Probability of dispersal from cell *j* to cell *i*
$\mathbf{D}$	Matrix of dispersal probabilities D_{ij}
K_x	Alongshore diffusivity ($m^2 \cdot s^{-1}$)
$K_{x\ max}$	Maximum offshore alongshore diffusivity ($m^2 \cdot s^{-1}$)
K_y	Cross-shelf diffusivity ($m^2 \cdot s^{-1}$)
$K_{y\ max}$	Maximum offshore cross-shelf diffusivity ($m^2 \cdot s^{-1}$)
L_x	Alongshore diffusive displacement (m)
L_y	Cross-shelf diffusive displacement (m)
PLD	Pelagic larval duration (days)
q	Uniform random variable
s_U	Standard deviation of U ($m \cdot s^{-1}$)
T	Precompetency larval duration (days)
T_c	Competency period (days)
Δt	Time-step (s)
U	Alongshore velocity ($m \cdot s^{-1}$)
V	Cross-shelf velocity ($m \cdot s^{-1}$)
y	Cross-shelf position (m)
y^*	Correction factor for cross-shelf gradient
y_{NS}	Cross-shelf distance at which nearshore flow parameters begin increasing linearly (m)
y_{OS}	Cross-shelf distance at which flow parameters take on maximum offshore values (m)
x	Alongshore position (m)
ξ	Larval mortality rate (day^{-1})
Entrainment calculations	
b	Probability of entrainment directly over CWIS intake
h	Mean depth at CWIS intake (m)
$P(r)$	Probability of entrainment at distance r from CWIS intake
Q_0	CWIS intake flux ($m^3 \cdot s^{-1}$)
r	Radial distance from CWIS intake (m)
r_0	Distance at which $P(r) = 0$ (m)
Population model	
α	Density-independent postsettlement survivorship
β	Maximum settler density ($settlers \cdot m^{-2}$)
C_i	Contribution of subpopulation i to the metapopulation
δ	Strength of Beverton–Holt density dependence
ϕ	Per capita adult fecundity ($eggs \cdot year^{-1}$)
$g(\phi, N_t)$	Density-dependent postsettlement survivorship function
$\lambda_{\mathbf{D}}$	Leading eigenvalue of $\mathbf{D}$
$N_{t,i}$	Population density at time t, location i ($individuals \cdot m^{-2}$)
$\overline{N}_{\bullet-i}$	Average population density of all patches except i
$\overline{N}'_{\bullet-i}$	Same as $\overline{N}_{\bullet-i}$, but calculated assuming 100% mortality at i
$S_{t,i}$	Settler density ($settlers \cdot m^{-2}$)
σ	Adult mortality rate ($year^{-1}$)
σ_{max}	Maximum value of σ for which population is persistent
$\Delta\tau$	Time-step ($year^{-1}$)
Traditional assessment statistics	
A	Number of adults produced in one time-step
AEL	Adult equivalent loss
d	Number of days larvae are exposed to entrainment
E_T	Total number of entrained larvae
f_i	Number of larvae hatched during survey i
LEP	Lifetime egg production
P_M	Proportional larval mortality
P_S	Proportion of source water sampled
PE_i	Proportion of larvae entrained during survey i

2009) — arguing for the necessity of capturing key features such as reduced flow nearshore.

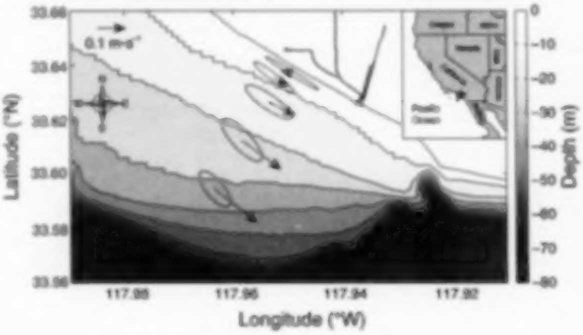
We refer to this nearshore region of reduced mean flow as a "coastal boundary layer" (Largier 2002, 2003, 2004). The coastal boundary layer (cross-shore scale of 10^3 m) is analogous to the classical small-scale turbulent boundary layers (scale of 10^{-2} m) observed at the interface of a fluid and a solid surface (Kundu and Cohen 2004). As coastal currents flow nearshore, the shoreline acts as a wall, constraining the magnitude and direction of the flow (Csanady 1972*a*, 1972*b*; Pettigrew and Murray 1986). In general, coastal currents are alongshore-polarized, with a relatively weak cross-shore component (Pettigrew and Murray 1986; Lentz 1994; Noble and Xu 2004). Further, the mean and variability in both alongshore and cross-shore flows are reduced toward the coast, and the coastal boundary restricts the extent of cross-shore diffusive motions (Largier 2002, 2003, 2004). Consistent with hydrodynamic theory, the flow speed must go to zero at the shore, as flow continuity precludes cross-shore flow and the no-slip boundary condition precludes alongshore flow. An example of this phenomenon can be seen in the cross-shore gradient of the mean velocity and standard deviation of the alongshore and cross-shore velocity components recorded off Huntington Beach, California (Fig. 2). While a strong cross-shore gradient in the standard deviation of the alongshore component of flow was not apparent during the time period represented by the data in Fig. 2, patterns consistent with our general description have been observed at other locations on the California coast (K.J. Nickols and J.L. Largier, unpublished data).

We represented the near-coastal reduction in mean flow velocities by making alongshore velocity U, alongshore diffusivity K_x, and cross-shore diffusivity K_y functions of the distance from shore, y. While the exact form of the cross-shore profile in currents in the coastal boundary layer varies from site to site (Largier 2003), there is usually a clear shoreward decrease that can be approximated by a linear relationship (current speed is related linearly to distance from the shore). In addition to this linear decrease, we note that (*i*) flows are likely to be more uniform offshore and (*ii*) one typically finds a very-nearshore zone where alongshore flows are blocked by coastal topography or driven by waves independent of the coastal boundary layer. Therefore, we used a trilinear function to characterize the very-nearshore coastal boundary layer and the offshore flow regions. Very-nearshore, uniform conditions are defined for areas directly adjacent to the coast to a distance y_{vn}, where the linear coastal boundary layer begins. This linear profile extends offshore to a distance y_{cbl}, beyond which the flow field is defined by a uniform, "free-stream" condition. Other functional forms for the attenuation of velocity toward the shore have been proposed, but at this time, insufficient data are available to justify a more complicated functional form, and preliminary studies with other functional forms exhibiting a nearshore flow reduction show qualitatively similar results. This is an ongoing area of research (K.J. Nickols and J.L. Largier, unpublished data).

Model CWIS description

We assume that the probability of particle entrainment by the CWIS is a function of radial distance from the intake location due to an approximately radial withdrawal flow structure near to the cooling water intake. Larvae that pass directly over the intake pipe will have a high likelihood of entrainment, whereas larvae passing the intake at a distance have a lower likelihood, and beyond a certain distance there is no chance of entrainment. Preliminary model runs using a variety of functions describing the entrainment probability showed that the functional form was not critical to model results. Consequently, we do not resolve the detailed flow structure in the near-field withdrawal zone but rather represent the probability of withdrawal around the CWIS by a cylindrical probability function. For a parcel of water located a radial distance r from the intake center, the probability of entrainment $P(r)$ is defined as

Fig. 2. Example of cross-shelf gradient in nearshore flow parameters observed at Huntington Beach, California. Velocity was measured using acoustic Doppler current profilers moored on the seafloor. Velocity data were averaged over entire water column. Arrows indicate direction and magnitude of mean velocity for the period 20 July – 30 September 2001. Ellipses indicate standard deviation in velocity over the same period along the major and minor principal axes of variation. Contour lines are 10 m isobaths. (Data is from L. Carillo, J. Largier, M. Noble, L. Rosenfeld, and P. Hamilton, unpublished data.)



$$P(r) = b\left(1 - \frac{r}{r_0}\right) \tag{6}$$

where $P(0) = b$ and $P(r_0) = 0$.

During the interval Δt = 120 s, the intake volume is $Q_0\Delta t$, where Q_0 is the intake volume flux (m^3·s^{-1}). The intake volume must equal the volume entrained from the coastal flow passing the intake pipe:

$$Q_0\Delta t = 2\pi h \int_0^{r_0} rP(r)\mathrm{d}r \tag{7}$$

where h is the mean water depth in the vicinity of the intake (h = 7 m in all model runs). Equation 7 can be solved to find r_0 for b = 1:

$$r_0 = \sqrt{\frac{3\Delta t Q_0}{\pi h b}} \tag{8}$$

To obtain an upper estimate of the effects of CWIS on benthic populations, we used Q_0 = 125 m^3·s^{-1}, which approximates the intake rate at the Diablo Canyon and San

Onofre nuclear generating stations, the two highest-flux CWIS on the California Coast (California Energy Commission 2005). For this scenario one obtains $r_0 = 45$ m.

Parameterization of flow scenarios for particle tracking model

There are three flow parameters that vary in the cross-shore dimension (U, K_x, K_y), and each is specified by four values that define the linear cross-shore profile: the cross-shore positions y_{vn} and y_{cbl}, the minimum value of the parameter (very-nearshore), and the maximum value of the parameter (offshore). In addition, one must specify the pelagic larval duration (PLD), the CWIS location, and intake volume flux Q_0. This is a high-dimensional system, and it is not realistic to conduct or communicate a systematic exploration of parameter space, nor a sensitivity analysis for the effect of each parameter value on entrainment and population dynamics. However, drawing on theory developed for homogenous flow environments (Siegel et al. 2003), we note that there are general nondimensional relationships between the advective and diffusive (stochastic) components of flow and the larval duration. If the ratio of the advective and diffusive components is expressed as the Peclet number (Largier 2003), it is clear that different combinations of flow parameters and larval durations with similar Peclet numbers can produce similar dispersal kernels (Supplemental Fig. S1[4]). A similar relationship between flow parameters and larval duration holds in the nonhomogenous flow scenarios (including a coastal boundary layer) that are modeled here. While we only present results from a few selected flow scenarios, we expect the dispersal kernels we show to vary in predictable ways with the relevant flow parameters; larger values of U will increase advective length scales, larger values of K_x and K_y will increase diffusive length scales, and longer PLD will increase the advective length scale (as in Supplemental Fig. S1[4]).

In practice, we chose a PLD of $T = 4$ days and $T_c = 2$ days (i.e., a 2-day window of competency beginning 4 days after spawning) to represent the relatively short PLDs of some nearshore species of conservation concern in California, such as abalones (*Haliotis* spp.; Hobday and Tegner 2002). This choice was also computationally expedient, as longer PLDs would have required prohibitively long computation times for the large number of simulations shown here. As noted above, longer PLDs would increase the advective length scales of the dispersal kernel in a nonlinear fashion (Supplemental Fig. S1[4]).

We first characterized the general effect of variability in parameters (within physically plausible bounds) on the shape of a dispersal kernel. We then selected two parameter sets that represent relatively low- and high-dispersal scenarios for analysis in the population model. It is reasonable to expect that population results under alternative flow scenarios would fall between these two more extreme scenarios. Thus we characterize the general effects of CWIS on populations under a range of conditions without conducting a fully orthogonal exploration of parameter space.

In general, we used parameter values that were scale estimates based on a review of literature (e.g., Largier 2003) combined with knowledge of both published and unpublished oceanographic data for coastal California (including drifter, dye, current meter, and high-frequency radar data). Though the parameters were drawn from studies in California, flow parameters of the same order of magnitude could be expected to occur in many other locations worldwide.

In the nearshore region ($y < y_{vn}$), we expect stalled or decoupled alongshore flow because of the drag of the shoreline, reefs, or kelp forests, the importance of wave-driven forcing in the surf zone, and the presence of coves, headlands, or stacks that obstruct the flow. Thus we assume $U_{min} = 0\ \mathrm{m{\cdot}s^{-1}}$ in this region. In the offshore region ($y > y_{cbl}$), velocity should be on the order of $U_{max} = 0.1\ \mathrm{m{\cdot}s^{-1}}$, but may range as high as $0.3\ \mathrm{m{\cdot}s^{-1}}$ in times of strong wind forcing (e.g., Lentz and Winant 1986; Largier et al. 1993).

Fluctuating alongshore currents (which account for alongshore eddy diffusivity K_x) are expected to have a structure similar to that of the alongshore mean flow, increasing linearly across the coastal boundary layer. We took $K_{x\ max} = 100\ \mathrm{m^2{\cdot}s^{-1}}$ as a scale that reasonably represents reversing flows on short time scales associated either with tides or with synoptic variability in the offshore region (flows of order $10^{-1}\ \mathrm{m{\cdot}s^{-1}}$ reversing on times scales of 10^5 s). Given that nearshore K_x is weak, but does not go to zero owing to wave-driven flows and topographic eddy effects, we used a value of $K_{x\ min} = 20\ \mathrm{m^2{\cdot}s^{-1}}$ (List et al. 1990; Clarke et al. 2005). However, alongshore mixing is typically dominated by shear dispersion due to mixing across the cross-shore shear in the alongshore flow; thus, the exact value of K_x is less important than the values for K_y and dU/dy.

Because we were using the dispersal kernels in a population model, we also attempted to represent flow variability on time scales longer than the synoptic scale described by K_x. Therefore, for each flow scenario we performed 10 different simulations in which U_{max} was drawn from a normal distribution with a standard deviation of s_U. We estimated s_U on the order of $0.1\ \mathrm{m{\cdot}s^{-1}}$ (Lentz and Winant 1986; Largier et al. 1993).

Cross-shore currents were assumed to have zero mean because of the shore boundary and fluctuations that decrease to zero at the shore. Again, we assumed a uniform very-nearshore zone because of wave-driven mixing and currents and used $K_{y\ min} = 1\ \mathrm{m^2{\cdot}s^{-1}}$ as a reasonable scale for surf zone mixing (Smith and Largier 1995; Clarke et al. 2005). We assumed that the maximum value in the offshore region was $K_{y\ max} = 100\ \mathrm{m^2{\cdot}s^{-1}}$, representing isotropic mixing away from the coastal boundary, but also considered smaller values of 10–30 $\mathrm{m^2{\cdot}s^{-1}}$ (representing weaker cross-shore mixing).

Depending on the roughness of the coastline and the nature of the surf zone, the width of the very-nearshore zone varies. We assumed that it should be on the order of $y_{near} = 100$ m but could range from 50 m (e.g., smooth shoreline and little waves) to as much as 500 m (e.g., in presence of headlands, kelp forests, and macro-rip currents). The offshore extent of the coastal boundary layer (the point at which free-stream shelf velocity is attained) may depend on the steepness of the shelf and larger-scale coastline features, as well as the strength of shoreline drag. We considered values ranging from $y_{cbl} = 1500$ to 6000 m based on measurements from coastal areas where a maximum "free-stream" alongshore velocity was observed (K.J. Nickols, unpublished data).

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[4] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

In exploring parameter space, we first varied the configuration of the linear profile representing the extent of the coastal boundary layer, allowing y_{vm} to take on values of 50, 100, or 200 m and y_{cbl} to be 1500, 3000, or 6000 m. In this analysis, we used $K_{y,max}$ = 100 m²·s⁻¹, U_{max} = 0 or 0.1 m·s⁻¹, and used the values given above for the other parameters. The resulting dispersal kernels revealed that the value of y_{vm} does not have a strong influence on the shape or displacement of the kernel (Supplemental Fig. S2[4]), but that both the advective and diffusive components of dispersal are reduced when the coastal boundary layer extends further offshore (larger values of y_{cbl}) in the case of nonzero U_{max}. Based on this analysis, we chose the intermediate values of y_{vm} = 100 m and y_{cbl} = 3000 m for further analysis.

We then further explored the effect of variation in U_{max} and $K_{y,max}$ on the shape of dispersal kernels (Figs. 3a–3c show the kernels produced by a range of values of these two parameters). Higher values of either parameter increase the rate of shear dispersion and thus the diffusive spread of dispersal. Based on this range of results, we chose two flow scenarios for further analysis in the population model: U_{max} = 0.1 m·s⁻¹ and $K_{y,max}$ = 10 m²·s⁻¹, representing a relatively low-dispersal scenario (hereafter, Scenario 1), and U_{max} = 0.2 m·s⁻¹ and $K_{y,max}$ = 30 m²·s⁻¹, representing a higher-dispersal scenario (hereafter, Scenario 2). The long-term persistence of a population requires some minimum fraction of larvae to return to the spawning location (Byers and Pringle 2006) — flow scenarios with more extreme values of these two flow parameters did not support persistent populations, even without CWIS entrainment, and thus were not appropriate scenarios for the study of CWIS impacts.

Population dynamics model

Nisbet et al. (1996) proposed a generic model to describe the dynamics of a benthic population that was exposed to CWIS entrainment:

$$(9)\qquad N_t = [\phi\alpha N_t \cdot g(\phi, N_t)] + N_t e^{-\sigma}$$

where N_t is population density at time t, ϕ is per capita adult fecundity, α is juvenile survivorship, σ is adult mortality, and g is a function describing the density-dependent survival of juveniles. This model can describe a population with a planktonic larval stage, but it is assumed that ϕ includes mortality during the larval stage and the probability of being transported offshore away from suitable settlement habitat in addition to true fecundity.

For many benthic populations, it is reasonable to assume g is a Beverton–Holt function (Nisbet et al. 1996; Quinn and Deriso 1999; Osenberg et al. 2002). We used the Shepherd function, a variant of Beverton–Holt that permits overcompensation (Shepherd 1982):

$$(10)\qquad g(\phi, N_t) = \frac{1}{1 + (\phi N_t/\beta)^\delta}$$

This function approaches unity when juvenile density ϕN_t is near zero and is equal to 0.5 when juvenile density = β (parameter β is a scaling constant determining the areal units over which density is defined; model results are completely insensitive to its value). The parameter δ controls the degree of compensation in the density-dependent mortality, ranging from density independence (δ = 0) to weak compensation (0 < δ < 1), exact compensation (δ = 1), and overcompensation (δ > 1; Supplemental Fig S3[4]).

Nisbet et al. (1996) assumed that larvae were well mixed within the spatial domain of the model, so that the population could be modeled as a single stock without spatial structure. After exploring a range of functional forms for intraspecific competition in their population model, they found that larval mortality due to CWIS entrainment was least likely to have a strong effect on the population if $g(\phi, N_t)$ were exactly compensatory (δ = 1), because entrained larvae were likely to have died anyway during postsettlement competition. Entrainment was most likely to have a disproportionate effect on population dynamics if $g(\phi, N_t)$ were strongly overcompensatory (δ > 1), so that the loss of entrained larvae would increase the survival of the remaining larvae. Overcompensatory dynamics should lead to a positive effect of entrainment on adult densities, but can also destabilize population dynamics, leading to an overall negative effect on the population (Nisbet et al. 1996).

We adapted the framework proposed by Nisbet et al. (1996) to represent a spatially structured metapopulation consisting of n subpopulations of sessile adults linked by dispersing larvae.

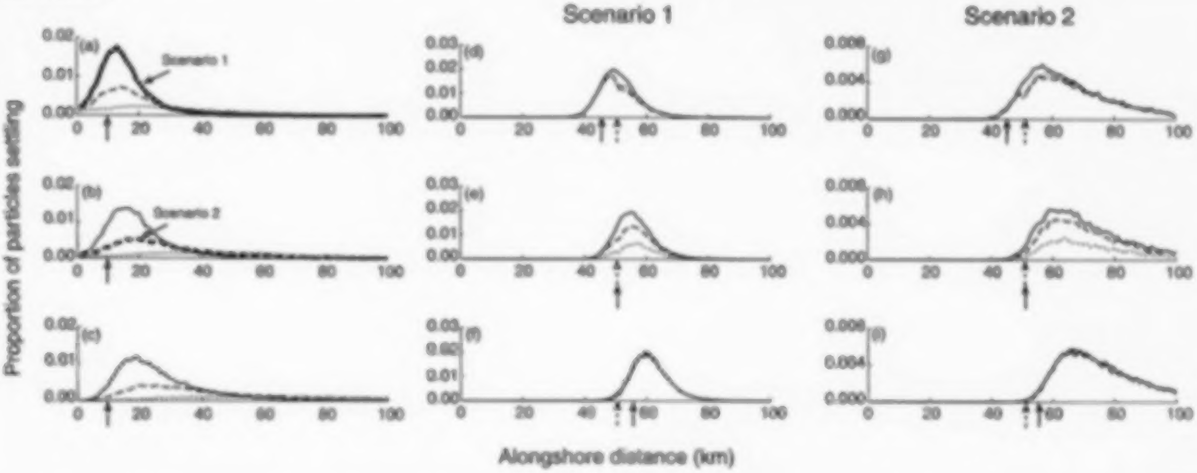
$$(11)\qquad S_{i,t} = \sum_{j=1}^{n} D_{ij}\phi N_{j,t}$$

$$N_{i,t+1} = \frac{\alpha}{1 + (S_{i,t}/\beta)^\delta} S_{i,t} + N_{i,t} e^{-\sigma}$$

Here the population dynamics are essentially the same as in eqs. 9–10, except that the density of settlers, S, arriving at subpopulation i in time t is the sum of larvae produced at all other locations j multiplied by the probability of dispersing from j to i, given by D_{ij}; and ϕ denotes true per capita adult fecundity (not including larval survival). The values D_{ij} make up the elements of the dispersal matrix **D**. Each column of **D** is the dispersal kernel from one cell. We assume that the dispersal matrix represents both natural larval mortality and the effects of CWIS entrainment, the values of which we estimate by simulating the movement of larvae with the particle tracking transport model. The time-step $\Delta\tau$ of this model is the interval between spawning events in the population (and required for settlers to become reproductive), provided that interval is longer than the 5-day PLD. Thus, $\Delta\tau$ could represent a weekly, monthly, annual, or greater time scale; for generality we take $\Delta\tau$ to be 1 year, but analyze equilibrium dynamics that are not sensitive to the value of $\Delta\tau$ relative to the PLD.

Directly simulating larval mortality when calculating **D** would have required a computationally infeasible number of Lagrangian particles, as the number of particles one must simulate to obtain a certain number of settlers increases by a factor of 10 for larval mortality of 90%. Therefore, we simulated the dispersal of 10^8 particles without mortality, but kept track of the time at which each successful particle "settled". We then calculated the probability that each particle would have lived to that age, given a constant larval

Fig. 3. Example dispersal kernels produced by particle tracking model, both (*a*–*c*) without entrainment and (*d*–*i*) with entrainment in a cooling water intake system (CWIS). Panels (*a*–*c*) display a range of dispersal kernels without entrainment, produced using values of maximum offshore velocity of (*a*) 0.1 $m\cdot s^{-1}$, (*b*) 0.2 $m\cdot s^{-1}$, or (*c*) 0.3 $m\cdot s^{-1}$ for a range of values of maximum cross-shelf diffusivity $K_{y\ max}$: 10 $m^2\cdot s^{-1}$ (solid line), 30 $m^2\cdot s^{-1}$ (dashed line), and 100 $m\cdot s^{-2}$ (dotted line). The trilinear profile representing the coastal boundary layer used values of $y_{\text{in}} = 100$ m and $y_{\text{out}} = 3000$ m; other flow parameters are as described in the text. Bold lines in (*a*) and (*b*) represent flow Scenarios 1 (low dispersal) and 2 (high dispersal), respectively, described in the text and used in the metapopulation model analysis. Panels (*d*–*i*) display dispersal kernels with CWIS entrainment for Scenario 1 (*d*–*f*) or Scenario 2 (*g*–*i*). Kernels were estimated with CWIS intake at 500 m offshore (dashed line) or 50 m offshore (dotted line); a kernel without intake (solid line) is shown for comparison. In all panels, 10^4 particles were released within 0.5 km of alongshore position indicated by solid arrow; the alongshore position of the CWIS in (*d*–*i*) is at 50.5 km, indicated by the dashed arrow. The height of the curve represents proportion of larvae spawned at the release point that settled at that location.



mortality rate ξ. The probability of dispersal from *i* to *j* was then calculated as the weighted sum of the number of particles that traveled from *i* to *j*, divided by 10^4 (the total number of particles released), where the weight for each particle is its survival probability.

Using this model, we also calculated the conservation value of different regions of the coastline using the deletion index method (White 2008). The deletion index is an estimate of the "contribution" (sensu Ovaskainen and Hanski 2003) of one subpopulation to the rest of the metapopulation and is defined as the proportional change in the abundance of individuals in the metapopulation if that subpopulation were removed:

$$(12)\qquad C_i = 1 - \frac{\overline{N}'_{\bullet-i}}{\overline{N}_{\bullet-i}}$$

where C_i is the contribution of subpopulation *i*, $\overline{N}_{\bullet-i}$ is the mean population density in all subpopulations except *i* under normal conditions, and $\overline{N}'_{\bullet-i}$ is the mean population density in all subpopulations except *i* under the assumption that all larvae arriving at *i* die instantly. This could represent habitat destruction, overharvesting, or other types of disturbance. The value of C_i ranges from 0 (no effect of removing *i*; i.e., it is a global sink) to 1 (the metapopulation does not persist without *i*; i.e., it is a global source). In our model, each subpopulation represented a 1 km segment of a 100 km linear coastline (see below for details on the spatial domain). Spatial patterns in C_i due to entrainment are only evident if C_i is calculated for relatively small subpopulations, but management decisions are typically made at spatial scales somewhat larger than the 1 km resolution of our model. We chose to calculate C_i by grouping subpopulations into 5 km sections of coastline. This spatial scale was more computationally efficient (fewer simulations of $\overline{N}'_{\bullet-i}$ were required) and represents an appropriate scale for spatial management, as it is comparable to the minimum size of MPAs in California (California Department of Fish and Game 2008).

Parameterization of population model

The fundamental requirement for population persistence is that every adult in a population replace itself with at least one offspring within its lifetime (Mace and Sissenwine 1993; Hastings and Botsford 2006). In a deterministic metapopulation model such as ours, in which there are no Allee effects, this criterion is equivalent to the requirement that the metapopulation will have a positive growth rate at very low population densities (i.e., when density dependence is unimportant). Hastings and Botsford (2006) showed that this requirement can be expressed as

$$(13)\qquad 1 \le \alpha\lambda_{\mathbf{D}}\phi + e^{-\sigma}$$

where α, ϕ, and σ are the same as in eq. 11, and $\lambda_{\mathbf{D}}$ is the leading eigenvalue of the dispersal matrix **D**. Given constant values for the other parameters, eq. 13 can be used to calculate the maximum adult mortality $\sigma_{\max}$ for population persistence (White 2010).

To ensure the generality of our results, we selected biologically plausible values for each demographic parameter (Table 2). Rather than focus on modeling a particular species, we performed a more general analysis by expressing

Table 2. Documented range of model parameters, when applicable, and values chosen for simulations in the paper.

Parameter	Range of values	Model value(s)	Reference
Particle tracking model			
$K_{x\ \min}$	~0–20 $\text{m}^2\cdot\text{s}^{-1}$	20 $\text{m}^2\cdot\text{s}^{-1}$	List et al. 1990, Clarke et al. 2005
$K_{x\ \max}$	100 $\text{m}^2\cdot\text{s}^{-1}$	100 $\text{m}^2\cdot\text{s}^{-1}$	List et al. 1990
$K_{y\ \min}$	1–10 $\text{m}^2\cdot\text{s}^{-1}$	1 $\text{m}^2\cdot\text{s}^{-1}$	Smith and Largier 1995, Clarke et al. 2005
$K_{y\ \max}$	10–100 $\text{m}^2\cdot\text{s}^{-1}$	10, 30 $\text{m}^2\cdot\text{s}^{-1}$	Davis 1985, Largier et al. 1993, Largier 2003
s_U	—	0.1 $\text{m}\cdot\text{s}^{-1}$	Lentz and Winant 1986, Largier et al. 1993
T	—	4 days	Hobday and Tegner 2002
T_c	—	2 days	Hobday and Tegner 2002
Δt	—	120 s	—
$U_{\min}$	0 $\text{m}\cdot\text{s}^{-1}$	0 $\text{m}\cdot\text{s}^{-1}$	Largier 2003, K.J. Nickols and J.L. Largier, unpublished data
$U_{\max}$	0–0.2 $\text{m}\cdot\text{s}^{-1}$	0.1, 0.2 $\text{m}\cdot\text{s}^{-1}$	Lentz and Winant 1986, Largier et al. 1993, K.J. Nickols and J.L. Largier, unpublished data
V	0 $\text{m}\cdot\text{s}^{-1}$	0 $\text{m}\cdot\text{s}^{-1}$	J.L. Largier, unpublished data, Lentz and Winant 1986
y_{in}	50–500 m	100 m	K.J. Nickols and J.L. Largier, unpublished data
y_{out}	1500–6000 m	3000 m	K.J. Nickols and J.L. Largier, unpublished data
ξ	—	0.2 day^{-1}	—
Entrainment calculations			
h	—	7 m	—
Q_0	3–125 $\text{m}^3\cdot\text{s}^{-1}$	125 $\text{m}^3\cdot\text{s}^{-1}$	California Energy Commission 2005
r_0	—	45 m	—
Population model			
α	—	0.5	—
β	—	1 $\text{settler}\cdot\text{m}^{-2}$	—
ϕ	—	10^5 $\text{eggs}\cdot\text{year}^{-1}$	—

the population dynamics in terms of the proximity of the population to the persistence threshold. Given the parameter values in Table 2, we calculated $\sigma_{\max}$ and simulated population dynamics using $\sigma = 0.25\sigma_{\max}$, $0.5\sigma_{\max}$, and $0.75\sigma_{\max}$, representing populations that range in their proximity to the persistence threshold. Higher values of σ (closer to $\sigma_{\max}$) could represent anthropogenic disturbances such as fishing, pollution, etc. We calculated $\sigma_{\max}$ using the value of λ_D derived from the dispersal matrix with no CWIS entrainment. This approach thus allowed us to examine the consequences of entrainment for populations that are healthy (low σ) and for those that are experiencing other anthropogenic disturbances (high σ). Because the value of $\sigma_{\max}$ accounts for the other demographic parameters, these general results are not sensitive to the particular values chosen.

We performed simulations with $\delta = 1$ (compensatory), which always produces a stable equilibrium, and $\delta = 1.5$ (overcompensatory), which could yield dampened oscillations (i.e., mild instability) at equilibrium, although in practice dynamics were stable with $\delta = 1.5$ given the range of other demographic parameters used. Natural fish and invertebrate populations vary greatly in the degree of compensation (Myers 2001; Wahle 2003), and eq. 10 is generally difficult to parameterize (Myers 2001), so exploring model results for these two values of δ permits a general exploration of the scope of model behavior for a range of plausible levels of compensation.

Traditional assessment protocols

We used the results of the coupled particle tracking and metapopulation models to calculate the traditional CWIS assessment statistics using the usual formulae. For these calculations we used the known number of entrained larvae (simulating a situation in which sampling is perfectly accurate). We then used the model results to calculate alternative metrics that capture the intended definition of the traditional statistics. These alternative "spatial" statistics reflect the importance of postsettlement density dependence and the spatial distribution of settlement.

Adult equivalent loss (AEL) is intended to reflect the number of adults that would have been produced by the entrained larvae. It is calculated as

$$\text{(14)} \qquad \text{AEL} = E_T\zeta$$

where E_T is the total number of entrained larvae, and ζ is the survivorship from the larval stage to adulthood. Typically this is calculated assuming that survivorship is purely density independent:

$$\text{(15)} \qquad \text{AEL}_{\text{trad}} = E_T\alpha\sigma$$

In this formulation, ζ has been replaced with terms for the survivorship through the settler and 1-year-old stages (assuming "adults" are ≥1 year old; see eq. 11). For simplicity we assume that most larval mortality happens before entrainment, but we could make the opposite assumption and also include the term ξ for larval survivorship.

We then also calculated the AEL in a way that explicitly accounts for the spatial patterns of settlement and density dependence. This simply requires taking the distribution of adults at equilibrium in an entrainment scenario and calculating for each location i the number of 1-year-olds at each location in the next time-step that would be obtained if entrainment were halted, A_{none}, and the number obtained if entrainment continues, A_{entrain}:

$$\text{(16)} \qquad \mathrm{AEL}_{\mathrm{spatial}} = \sum_i (A_{\mathrm{none},i} - A_{\mathrm{entrain},i})$$

Fecundity hindcasting (FH) is intended to relate the number of larvae entrained to the number of adult females required to produce that number of larvae. The intent is to find the number of females that are effectively removed from the population by entrainment. Here a key value is the lifetime egg production (LEP) of one adult, which is the per capita annual fecundity multiplied by the mean lifespan of a recruit (LEP = ϕ/σ; we assume without loss of generality that all adults can produce eggs; this could either describe an hermaphroditic population or require that ϕ is scaled by half). Given that value

$$\text{(17)} \qquad \mathrm{FH}_{\mathrm{trad}} = E_{\mathrm{T}}/(\mathrm{LEP}\,\xi)$$

where E_{T} is the number of entrained larvae, and ξ is larval survivorship. Note that this assumes that larval mortality takes place before entrainment, just as above in the AEL calculation. It does not actually matter whether we assume that larval mortality takes place before or after entrainment, so long as the same assumption is made for both statistics.

The conceptual weakness of this measure is that because of compensatory density-dependent mortality, one could actually remove quite a large number of reproductive females from the population before noticing an effect in the number of successful recruits. Therefore, it may be more informative to consider the number of successful recruits removed from the population and calculate the equivalent number of females needed to produce that many recruits. The calculation then becomes

$$\text{(18)} \qquad \mathrm{FH}_{\mathrm{spatial}} = \mathrm{AEL}_{\mathrm{spatial}}/(\mathrm{LEP}\,\xi\alpha\sigma)$$

This calculation takes the number of adult equivalents lost from the population, removes the effects of postsettlement density-independent survivorship, and divides by LEP.

The empirical transport model (ETM) calculation is designed to extrapolate the total larval loss at the cooling water intake from several samples of the larval population within the source water (Boreman et al. 1981). The formula is

$$\text{(19)} \qquad P_{\mathrm{M}} = 1 - \sum_{j=1}^{n} f_j (1 - P_{\mathrm{S}}\,\mathrm{PE}_j)^d$$

where P_{M} is proportional mortality, PE_j is the estimate of proportional larval entrainment during the jth survey, f_j is the number of larvae hatched during the jth survey, d is the number of days larvae are exposed to entrainment mortality, and P_{S} is the proportion of the entire source water population that was actually sampled. We used the difference between settlement in non-entrainment and entrainment scenarios to calculate the actual value of P_{M} in the spatial model. Just as in the AEL calculation, this requires finding the distribution of population density at equilibrium, then calculating the number of settlers obtained in the next time-step if entrainment continues (S_{entrain}) or if it is suddenly halted (S_{none}):

$$\text{(20)} \qquad P_{\mathrm{M\ spatial}} = 1 - S_{\mathrm{entrain}}/S_{\mathrm{none}}$$

Given the value of $P_{\mathrm{M\ spatial}}$ in each scenario, it is straightforward to see whether there is any relationship between that statistic and the actual effect of entrainment on the population in the spatial model.

Results

Effects of entrainment on dispersal patterns

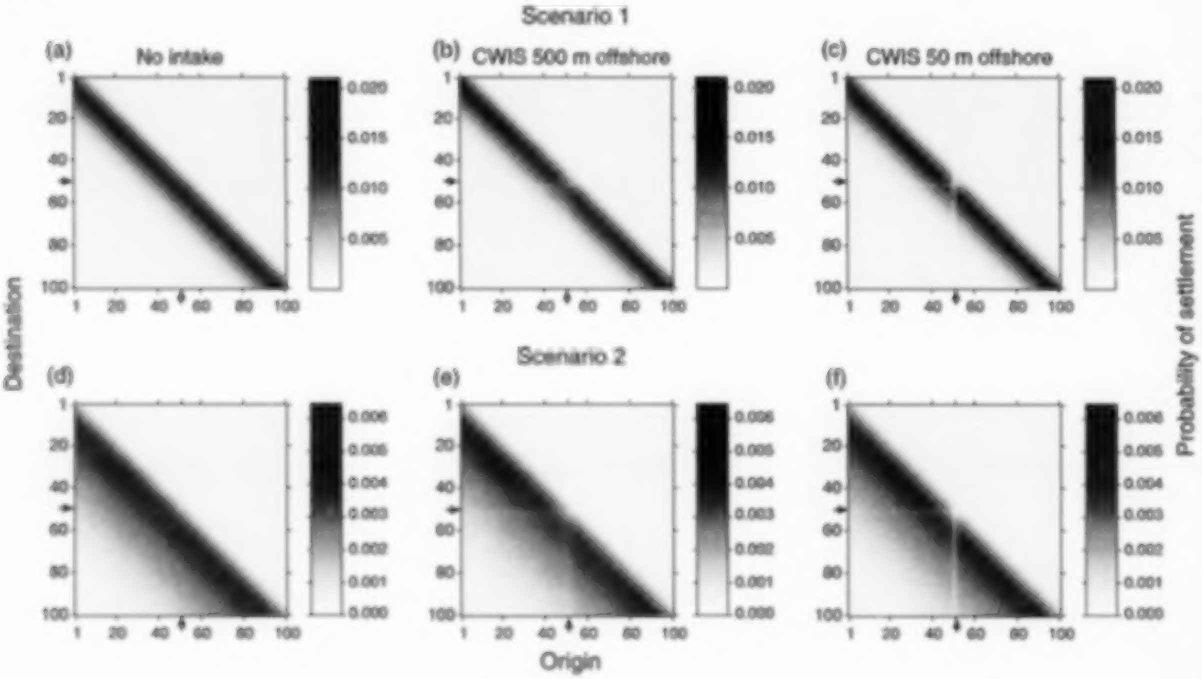
The effect of CWIS entrainment on dispersal patterns varied between flow scenarios and as a function of spawning location, as seen in several representative dispersal kernels (Figs. 3*d*–3*i*). In Scenario 1 (low dispersal), there was essentially no effect of entrainment on dispersal probabilities for larvae spawned ≥10 km upstream (not shown) or ≥5 km downstream (Fig. 3*f*) of the CWIS. There was a slight reduction in the probability of settlement in the vicinity of the CWIS for larvae spawned 5 km upstream of the intake, and this reduction was similar for both offshore locations of the CWIS (Fig. 3*d*). For larvae spawned directly adjacent to the CWIS, however, entrainment reduced the probability of dispersal to all other locations. This reduction was greater when the CWIS was 50 m offshore than when 500 m offshore (Fig. 3*e*). Similar patterns held in Scenario 2 (high dispersal), although the tails of these kernels were much longer and the mode of the kernel was shifted downstream. Similar to Scenario 1, there was no effect of entrainment far upstream (not shown) or downstream of the CWIS (Fig. 3*i*), a slight reduction in settlement near the CWIS for larvae spawned several kilometres upstream (Fig. 3*g*), and a large reduction in dispersal to all locations for larvae spawned near the CWIS, especially when the CWIS was 50 m offshore (Fig. 3*h*).

The spatial distribution of entrainment effects can be visualized more completely by examining the entire dispersal matrix **D** for each scenario (Fig. 4; shown in color for greater clarity in Supplemental Fig. S4[4]). Two distinct effects of entrainment are apparent (Fig. 4). The first is a reduction in settlement near the CWIS from origins upstream. This is evident as a horizontal band of reduced dispersal probabilities near x = 50 km (Fig. 4). The second is a reduction in dispersal to all locations from origins in the vicinity of the CWIS. This is evident as a vertical band of reduced probabilities near x = 50 km. Reductions in dispersal both to and from the vicinity of the CWIS were greater when the CWIS was 50 m offshore than when it was 500 m offshore.

Effects of entrainment on population dynamics

The population-level effects of entrainment depended heavily on the value of σ; i.e., the proximity of the population to collapse in the absence of entrainment. We first consider Scenario 1 with compensatory density-dependent mortality (δ = 1). When adult mortality was low ($\sigma = 0.25\sigma_{\max}$ or $0.5\sigma_{\max}$), there was a slight reduction in larval settlement in the vicinity of the CWIS (the offshore position of the CWIS had little effect on this result), but because postsettlement mortality was compensatory, the remaining settlers had a slightly higher survival rate, and there was no substantial effect on the adult population (Figs. 5*a*, 5*b*). When the population was nearer to collapse ($\sigma = 0.75\sigma_{\max}$), population densities were much lower and shifted downstream, even without entrainment, because larval production

Fig. 4. Dispersal matrices showing the effects of entrainment in a cooling water intake system (CWIS). Each panel shows the dispersal matrix for a different entrainment scenario. Spawning locations (origins) are on the columns; destinations are on the rows. Shading indicates the probability of dispersal from an origin to a destination. Results are shown for both Scenario 1 (*a–c*) and Scenario 2 (*d–f*); flow parameters associated with these scenarios are described in the text. The alongshore position of the CWIS was at the midpoint of the 51st spatial cell, indicated by arrows. The offshore location of the CWIS was either 500 m (*b*, *e*) or 50 m (*c*, *f*). In panels (*a* and *d*), there was no CWIS intake.

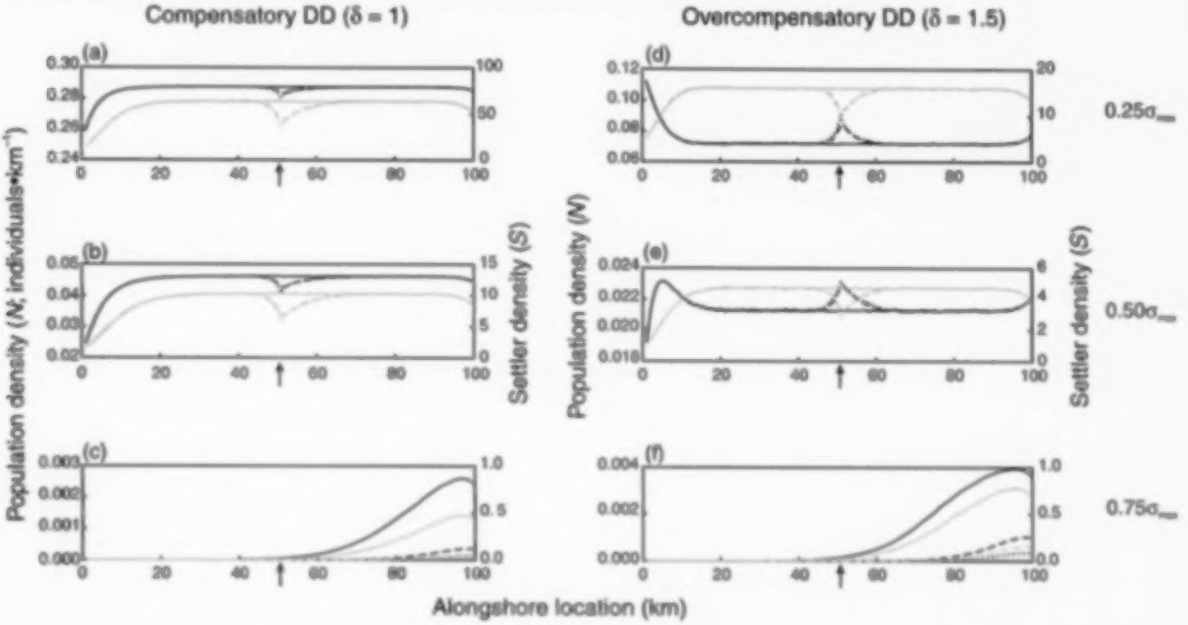


was only barely sufficient to offset the net advection of larvae (Fig. 5*c*; cf. Byers and Pringle 2006). In this scenario, entrainment had the effect of reducing overall larval settlement and population density at all locations. The spatial distribution of patch contribution values (*C*) was also affected by CWIS entrainment. For low adult mortalities ($\sigma = 0.25\sigma_{max}$; Fig. 6*a*), entrainment caused *C* to drop slightly near the CWIS, indicating a reduced metapopulation contribution from that area. *C* increased slightly upstream of the CWIS, suggesting that larval production in that region became more important to the rest of the population, likely because it was replacing entrained larvae that were spawned near the CWIS. However, the higher values of *C* upstream of the CWIS were still lower than the highest values of *C* in the domain, which always occurred near the upstream edge of the domain. The subpopulations there "anchored" the rest of the metapopulation, and the entire population would shift downstream somewhat if those locations did not contribute larvae to the system (similar results for *C* were obtained for $\sigma = 0.50\sigma_{max}$; Supplemental Fig. S5*a*[4]). The effects of entrainment on *C* were amplified in the near-collapse population ($\sigma = 0.75\sigma_{max}$; Fig. 6*b*), with conservation values approaching $C = 1$ (i.e., a global source) for locations upstream of the CWIS.

The remainder of the population modeling results can best be understood by comparison with Scenario 1 with compensatory density dependence. When mortality was overcompensatory in Scenario 1, the reduction in settlement near the CWIS (and at the upstream edge of the metapopulation) resulted in higher, not lower, adult population densities when σ was low, because postsettlement survival rates were higher with fewer settlers (Figs. 5*d*, 5*e*). As a result, entrainment increased patch contribution values near the CWIS and reduced *C* upstream of the CWIS (Fig. 6*d*; similar results for $\sigma = 0.50\sigma_{max}$ shown in Supplemental Fig. S5*d*[4]); this is opposite to the pattern for compensatory density dependence. When σ was near σ_{max} and the population was near collapse, the results were much more similar to the compensatory mortality case (Figs. 5*f*, 6*e*). This is because adult and settler densities were so low that the form of density dependence no longer had an effect on dynamics near equilibrium.

The results for Scenario 2 were very similar to those for Scenario 1 when adult mortality was low ($\sigma = 0.25\sigma_{max}$ or $\sigma = 0.5\sigma_{max}$), with the exception that settler densities were somewhat lower near the upstream edge of the population as a consequence of the higher rate of larval advection (Supplemental Fig. S6[4]; note that this produced either lower or higher adult density, depending on the form of density dependence). The effect of entrainment on patch contribution values had a similar spatial pattern but a much smaller magnitude than in the equivalent cases for Scenario 1 (Supplemental Fig. S5[4]). A more striking departure from Scenario 1 occurred when adult mortality was very high ($\sigma = 0.75\sigma_{max}$). In this case, population densities were very low and shifted

Fig. 5. Population model results for flow Scenario 1. Each panel shows the equilibrium distribution of larval settlers (gray lines) and adults (black lines) for compensatory (*a*–*c*) or overcompensatory (*d*–*f*) density-dependent (DD) postsettlement mortality. Adult mortality was 25%, 50%, or 75% of the value σ_{max} at which the population is no longer persistent. Results are shown for no CWIS entrainment (solid lines), CWIS at y = 500 m offshore (dashed lines), and CWIS at y = 50 m offshore (dotted lines). The alongshore location of the CWIS was 50.5 km, indicated by arrows. Note that vertical axis scales vary among panels.



far downstream even without entrainment, and entrainment drove population densities even closer to zero, effectively causing population collapse (Figs. 6*c*, 6*f*). This produced a very different pattern of patch contribution values; patch contribution was close to 1 for most locations in the absence of entrainment, indicating that each subpopulation made an essential contribution to the persistence of the entire metapopulation. In the presence of entrainment, contribution values were somewhat reduced near the CWIS when the CWIS was 50 m offshore, but not for 500 m offshore.

Traditional assessment protocols

We used the particle tracking and population model outputs to compare the estimates of AEL and FH statistics calculated using the "traditional" formulae (based on the number of larvae lost to entrainment in one model year at equilibrium) and the equivalent "spatial" values (i.e., the actual difference in number of adults and female fecundity between entrainment and non-entrainment model runs at equilibrium). We also report the proportional larval mortality P_M due to entrainment; this is equivalent to the value estimated by ETM calculations. We display these comparisons for both types of density dependence in Scenario 1 only (Fig. 7). The patterns for Scenario 2 were qualitatively very similar to these results (full set of statistics in Supplemental Table S1[4]).

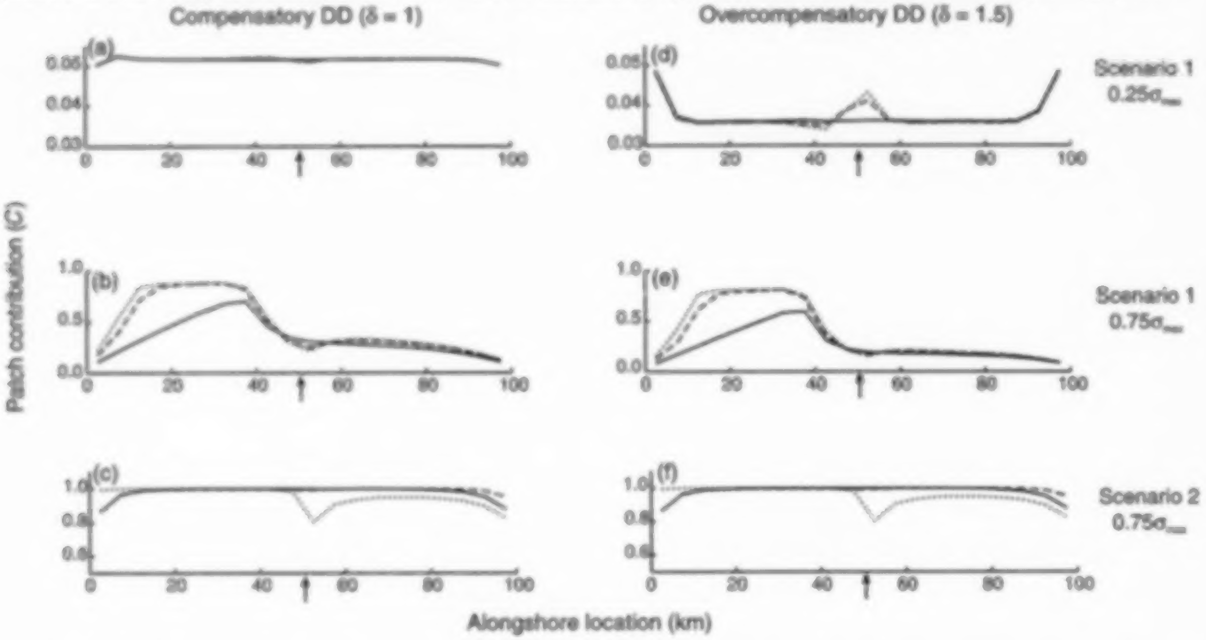
When adult mortality was relatively low ($\sigma = 0.25\sigma_{max}$ or $0.5\sigma_{max}$), the traditional estimates of AEL and FH were vastly greater than the spatial values calculated from the population model (Figs. 7*a*, 7*b*, 7*d*, 7*e*; the bars for AEL_{actual} and FH_{actual} are near zero and barely visible in these panels). The difference between traditional and spatial values was somewhat less when adult mortality was very high ($\sigma = 0.75\sigma_{max}$) in Scenario 1 (Figs. 7*c*, 7*f*), and the two estimates were nearly identical when the metapopulation was on the verge of collapse with high adult mortality in Scenario 2 (Supplemental Table S1[4]).

For P_M, we did not distinguish between traditional and spatial estimates because we assumed that empirical estimates of P_M should be at least proportional to the value calculated directly from the model output. Nonetheless, it is instructive to examine the relationship between P_M and population persistence, since ETM analyses are used to examine the effect of entrainment on populations, with the assumption that higher values of P_M indicate a higher biological impact. However, values of P_M were consistently higher when the adult population had lower mortality than when adult mortality was high and the population was near collapse (Figs. 7*g*, 7*h* versus Fig. 7*i*). This contrasts with the effect of entrainment on adult population density, for which there is a much greater effect in the high adult mortality scenario (Fig. 5).

Discussion

In general, our model results indicate that the ecological effects of CWIS entrainment are highly localized in space, even in the presence of strongly advective flows. This result is suggested by the effect of entrainment on dispersal probabilities and confirmed by simulations of benthic population dynamics showing that entrainment has minimal effects on

Fig. 6. Conservation value of patches in flow Scenario 1 (*a–b*, *d–e*) and Scenario 2 (*c*, *f*). Each panel shows the distribution of metapopulation contribution (*C*) values for compensatory (*a–c*) or overcompensatory (*d–f*) density-dependent (DD) postsettlement mortality. *C* was calculated for 5 km wide units of the coastline. Higher values of *C* indicate that a patch makes a larger contribution to the persistence of the rest of the metapopulation (maximum = 1). Adult mortality was 25% or 75% of the value $\sigma_{\max}$ at which the population is no longer persistent. Results are shown for no CWIS entrainment (solid lines), CWIS at $y = 500$ m offshore (dashed lines), and CWIS at $y = 50$ m offshore (dotted lines). The alongshore location of the CWIS was 50.5 km, indicated by arrow. Note that vertical axis scales vary among panels.



population densities except when the population has been heavily depleted by other factors. Based on our results, we conclude that future entrainment evaluation efforts should include spatially explicit population modeling and should not necessarily assume that entrainment effects are distributed across an entire metapopulation. Our spatially explicit approach contrasts prior studies that investigated CWIS effects using purely nonspatial models (Jensen and Hamilton 1982; Summers 1989; Nisbet et al. 1996) and those that resolved one- or two-dimensional circulation patterns to estimate rates of entrainment but used a nonspatial population model (Polgar et al. 1988; Heimbuch et al. 2007*a*, 2007*b*). Of course the latter approach remains appropriate for wide-ranging, non-site-attached species.

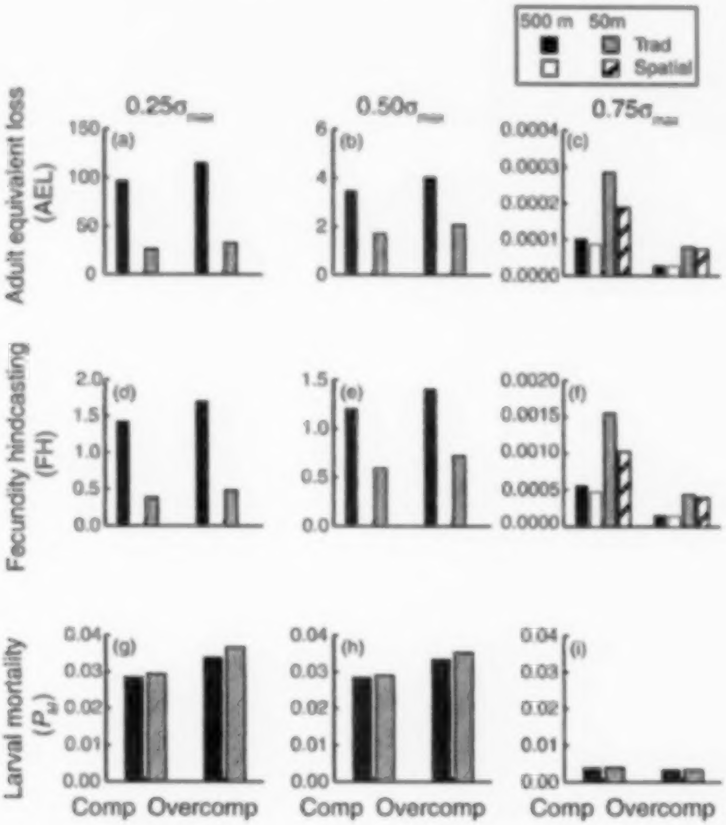
Here we focused specifically on the problem of entrainment in power plant cooling structures, but the general results of our models could apply to any case in which larvae suffer high mortality in a particular location on the inner shelf. This of course includes entrainment in other types of intake structures, such as those for desalination plants, but should also apply to natural sources of mortality. One such factor could be predation by nearshore planktivorous fishes or filter-feeding invertebrates, which will also tend to be highly localized and patchily distributed in nearshore kelp forests and reefs (the so-called "wall of mouths;" *e.g.*, Gaines and Roughgarden 1987; Hamner et al. 1988). These results may also extend to some degree to larval mortality due to exposure to concentrated contaminants in runoff plumes or hypoxia resulting from nearshore algal blooms (Morgan 1995). However, these latter effects would be associated with the presence of multiple water masses (i.e., freshwater plumes, upwelled water) and fronts between them. Such features were not included in our simple model of nearshore circulation, so caution should be used in extending our results to those sources of mortality.

Effects of entrainment on dispersal patterns

Entrainment had two distinct effects on larval dispersal patterns. First, larvae spawned anywhere along coast origins were entrained as they neared the coast at the CWIS intake, reducing settlement in the vicinity of the intake. Second, larvae spawned inshore of the intake were entrained as they moved offshore after spawning. Both effects were more severe when the CWIS intake was closer to shore, especially the entrainment of recently spawned larvae. Very close to shore, larvae are young and in high concentrations, and entrainment shortly after spawning is amplified by the low rates of diffusive movement very nearshore.

These specific results depend somewhat on our assumptions about nearshore circulation (although note that the high concentration of larvae nearshore will occur even if the coastal boundary has a minimal effect on dispersal). However, our exploratory analyses revealed that the general dispersal patterns (and presumably entrainment patterns) were robust to variation in the nearshore circulation parameters within the range of values appropriate for coastal California. The effects of variation in the alongshore velocity (U) and diffusivity (K_x and K_y) appear to be systematic and

Fig. 7. Comparison of traditional entrainment impact assessment metrics, calculated using the standard formulae ("Trad") and the actual values derived from model output ("Spatial"). Results shown are for Scenario 1 only. Adult mortality was 25%, 50%, or 75% of the value σ_{max} at which the population is no longer persistent. Postsettlement density-dependent mortality was either compensatory ($\delta = 1$; "Comp") or overcompensatory ($\delta = 1.5$; "Overcomp"). Bars that are not visible in (*a*–*f*) are very near zero; actual values are given in Table S1; refer to Supplementary data available online at cjfas.nrc.ca. No distinction was made between traditional and spatial calculations for larval mortality (P_M).



predictable: lower-flow scenarios (low *U* and *K* values) will be more like Scenario 1, with highly localized dispersal; higher values of *U*, *K*, or both will produce more diffuse dispersal like Scenario 2. Our method of describing nearshore flow encapsulates the general patterns outlined by Largier (2003, 2004) and should be reasonable; other work is underway to determine proper representations of functional forms for each parameter (K.J. Nickols, unpublished data). However, by exploring a variety of parameter sets, our results captured a range of possible coastal conditions found in areas affected by CWIS entrainment.

Effects of entrainment on population dynamics

The relatively large effects of entrainment on the probability of dispersal to and from the vicinity of the CWIS intake translated into minimal population-level effects for healthy, unexploited populations. Either the reductions in settlement resulting from larval loss were compensated by directly density-dependent mortality or contributed to a slight uptick in adult density if there was overcompensatory density dependence. However, for high rates of adult mortality (i.e., $\sigma_{0.75}$, which produces a near-collapse population), settlement rates were so low that dynamics were linear, and density dependence no longer played a role. In that case, entrainment could actually lead to population collapse.

The difference in entrainment effects depending on adult mortality scenario is easily understood in the context of two types of population persistence. When adult mortality is low and each location has high LEP, each individual deme is self-persistent, i.e., can exist in isolation and is not dependent on input from other demes (Hastings and Botsford 2006; Botsford et al. 2009; White et al. 2010*a*). In this case, reduced larval contribution from other sites has little effect on any subpopulation; this population has high resilience. This is also evident in the pattern of *C*, patch contribution value; each subpopulation has low *C* and entrainment changes this value very little. An alternative situation is network persistence, in which no subpopulation produces enough larvae to replace itself and be self-persistent; the entire system depends on replacement via connectivity among subpopulations over multiple generations (Hastings and Botsford 2006). In this case, removal of any one subpopulation can disrupt the persistence of the entire metapopulation by interrupting replacement pathways between other subpopulations. In the extreme (Scenario 2), each subpopulation has $C = 1$, so every component is essential, and reducing the contribution of any of them via entrainment can drive the population to collapse.

The finding that entrainment effects depend on levels of adult exploitation is not limited to spatially explicit population models. Jensen and Hamilton (1982) applied a fishery stock model to a population in Lake Erie and found that the effects of CWIS entrainment were lower if either adult mortality or fishing rates were lower. Heimbuch et al. (2007*b*) used a numerical circulation model to estimate the localized effects of entrainment on Atlantic menhaden, *Brevoortia tyrannus*, in New York's East River and coupled those estimates to a nonspatial population dynamics model. They found that entrainment effects were minimal relative to the effects of fishing, such that entrainment would only affect population dynamics if the population had been driven to low levels by fishing, as in our model.

Both population persistence and patch contribution values were also affected by the flow environment, although not to the degree that they were affected by adult mortality rates. When reproductive output was very low relative to advection (i.e., high adult mortality), populations grew closer to being swept downstream, out of the 100 km habitat domain. This effect is a general feature of population dynamics in an advective environment and occurs when both total reproductive output and the probability of local retention of larvae (D_{ii}) are low enough that the adult population in a cell is not replaced by incoming larvae and eventually goes extinct (Gaylord and Gaines 2000; Pachepsky et al. 2005; Byers and Pringle 2006). Under these conditions, "upstream" edges become increasingly important as anchor points to replenish downstream subpopulations (Gaylord and Gaines 2000; Gaines et al. 2003). If their reproduction is removed (e.g., by fishing or disturbance), then the entire population could shift downstream some distance. Thus, high values of C were associated with upstream subpopulations, especially in scenarios with high adult mortality and high flow. Consequently, as populations approach the persistence threshold — because of either environmental or anthropogenic factors — there is greater need to protect upstream subpopulations in general. This need is amplified in the presence of CWIS entrainment, which reduces the local retention and downstream export of subpopulations near the CWIS. Upstream subpopulations must produce sufficient larvae to offset those losses if the subpopulations downstream of the CWIS are to persist.

Contribution values could inform conservation and management decisions near CWIS, such as the placement of MPAs. In general, locations with high C values should be protected at the expense of regions with low C values. For example, as described above, MPAs should be placed outside of the radius of CWIS entrainment (on the order of a few kilometres) and preferably upstream of CWIS intakes. We refrain from making any specific recommendations regarding preferred MPA size or placement, as MPA performance depends on a variety of other factors beyond CWIS entrainment (White et al. 2010*a*, 2010*b*). Furthermore, our results were obtained using single-species models, but spatial management is typically intended to be ecosystem-based (Arkema et al. 2006). Thus one should consider joint estimates of C across multiple species, perhaps weighted by economic value or some other metric (White et al. 2010*b*), and potentially account for species interactions that could reverse the predictions of single-species models (Baskett et al. 2007; White 2008).

Usefulness of traditional assessment protocols

It is possible to draw several conclusions regarding the traditional entrainment statistics. Firstly, AEL and FH are not reliable indicators of entrainment effects. Because the total concentration of larvae in the water column, and thus the total number of entrained larvae, are greater when the population is healthy, both AEL and FH are higher for healthy populations than for populations near collapse, regardless of entrainment effects. Moreover, higher entrainment rates drive population densities (and thus larval production) down somewhat, so if AEL and FH are estimated at or near equilibrium (after the effects of entrainment have been felt in adult population densities), both values will be lower when entrainment has a greater population effect.

Secondly, the values of AEL and FH calculated assuming there is no postsettlement density dependence (the standard approach) are incorrect by several orders of magnitude when density dependence is strong. This is because many of the entrained larvae would have died anyway upon settlement because of intraspecific competition. When the population is near collapse, however, population densities are much lower and density-dependent mortality is far less strong, so the traditional AEL and FH calculations are reasonably accurate. Fortunately, then, the statistics are most accurate for situations in which population persistence is most sensitive to entrainment effects. However, it is impossible to tell from AEL and FH alone whether the population is near the collapse point.

For these reasons, there is great merit to the approach of Heimbuch et al. (2007*b*), who incorporated CWIS effects into a traditional stock assessment model parameterized in terms of spawning stock biomass (SSB). This approach allows a manager to determine how close a stock is to the persistence threshold and directly evaluate the relative contribution of entrainment to the overall reduction in SSB by fishing or other factors. In the Atlantic menhaden case study used by Heimbuch et al. (2007*b*), the effects of entrainment were quite minimal relative to other sources of stock depletion. Their approach was highly appropriate for a species such as Atlantic menhaden, which is highly mobile in the adult phase and readily modeled as a single well-mixed stock. In the case of a sessile adult phase like that which we modeled, it is not possible to reduce stock status to a single value such as SSB, because entrainment impacts (and possibly spatially variable fishing effects) may be distributed unevenly in space. This necessitates a spatially explicit approach. Nonetheless, our approach operates in the same spirit as that of Heimbuch et al. because we expressed population status relative to the population persistence threshold. Note that LEP in our calculations is essentially equivalent to SSB (O'Farrell and Botsford 2005; Kaplan et al. 2006), and both modeling approaches provide a means to nondimensionalize the life history by expressing population status relative to a persistence threshold.

Estimates of larval entrainment mortality, P_M, were generally higher in scenarios with higher intake rates. However, as with AEL and FH, there is no real relationship between P_M and population-level effects of entrainment. Values of P_M were quite similar for scenarios with healthy populations and near-collapse populations, yet larval mortality has a much greater potential effect on near-collapse populations. Thus, P_M does not necessarily convey information about the effect of mortality on population persistence. More importantly, within the set of near-collapse scenarios, P_M was sometimes higher for cases in which the population was persistent than for cases in which entrainment caused population collapse. Therefore, P_M itself is not diagnostic of population-level entrainment effects. This is because a point estimate of total larval mortality is not necessarily meaningful when the effects of that mortality (reduced larval settlement) are distributed in space.

Management implications

The results of our general strategic model suggest that the spatially localized effects of entrainment on larval dispersal have minimal, localized effects on adult populations, except when the population is subject to high rates of adult mortality due to other sources of exploitation, in which case entrainment can lead to population collapse. Importantly, the dependence of entrainment effects on external factors and the overall status of the population relative to the persistence threshold are not revealed by the linear approximations employed by traditional assessment protocols. Traditional assessments can be accurate when the population is near collapse and dynamics are in fact linear, but it is impossible to know if that is the case based on the assessment protocols alone.

Consequently, applying the lessons of this modeling effort to a more specific, tactical management scenario requires two major steps. First, it is important to quantify population status relative to the persistence threshold to place assessments in the proper management context. Our results suggest it may be reasonable to assume a priori that there is little effect of CWIS entrainment on most healthy populations, so overall population status should be assessed before proceeding with more sophisticated CWIS assessments. If the population appears to be threatened, the second step in an effective management strategy would be the development of a spatially explicit dispersal and population model like the one formulated here. While our model was rather generic, a more tactical model would require modifying the oceanographic and demographic model parameters to reflect the study system of interest. It would likely also be necessary to account for spatial variability in non-CWIS exploitation (such as in the case of MPAs) as well as nonlinearities in the coastline. Finally, because CWIS intakes are typically located quite near shore, where many larvae both begin and end their dispersal period, tactical assessments of entrainment impacts must include realistic representations of nearshore flows, and further work is needed to understand circulation near the coastal boundary.

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A hierarchical model to estimate the abundance and biomass of salmonids by using removal sampling and biometric data from multiple locations

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Abstract: We present a Bayesian hierarchical model to estimate the abundance and the biomass of brown trout (*Salmo trutta fario*) by using removal sampling and biometric data collected at several stream sections. The model accounts for (*i*) variability of the abundance with fish length (as a distribution mixture), (*ii*) spatial variability of the abundance, (*iii*) variability of the catchability with fish length (as a logit regression model), (*iv*) spatial variability of the catchability, and (*v*) residual variability of the catchability with fish. Model measured variables are the areas of the stream sections as well as the length and the weight of the caught fish. We first test the model by using a simulated dataset before using a 3-location, 2-removal sampling dataset collected in the field. Fifteen model alternatives are compared with an index of complexity and fit by using the field dataset. The selected model accounts for variability of the abundance with fish length and stream section and variability of the catchability with fish length. By using the selected model, 95% credible interval estimates of the abundances at the three stream sections are (0.46,0.59), (0.90,1.07), and (0.56,0.69) fish/m^2. Respective biomass estimates are (9.68, 13.58), (17.22, 22.71), and (12.69, 17.31) g/m^2.

Résumé : Nous présentons un modèle hiérarchique bayésien pour estimer l'abondance et la biomasse de truites brunes (*Salmo trutta fario*) basé sur un échantillonnage par retraits et des données biométriques récoltées sur plusieurs sections de cours d'eau. Le modèle tient compte de (*i*) la variabilité de l'abondance en fonction de la longueur des poissons (comme une distribution de mélange), (*ii*) la variabilité spatiale de l'abondance, (*iii*) la variabilité de la capturabilité en fonction de la longueur du poisson (comme modèle de régression logit), (*iv*) la variation spatiale de la capturabilité et (*v*) la variabilité résiduelle de la capturabilité en fonction des poissons. Les variables mesurées du modèle incluent les surfaces des sections de cours d'eau, ainsi que la longueur et la masse des poissons capturés. Nous testons le modèle à l'aide d'une banque de données simulées avant d'utiliser un ensemble de données récoltées à trois sites et en deux échantillonnages par retraits en nature. Nous comparons quinze modèles de rechange avec un indice de complexité et d'ajustement aux données de terrain. Le modèle retenu tient compte de la variabilité de l'abondance en fonction de la longueur des poissons et de la section de cours d'eau, ainsi que de la variabilité de la capturabilité en fonction de la longueur des poissons (sans la variabilité spatiale ou résiduelle de la capturabilité). Dans le modèle retenu, les estimations de l'intervalle crédible au niveau de 95 % de l'abondance dans les trois sections de cours d'eau sont (0,46; 0,59), (0,90; 1,07) et (0,56; 0,69) poissons/m^2. Les estimations de biomasses correspondantes sont (9,68; 13,58), (17,22; 22,71) et (12,69; 17,31) g/m^2.

[Traduit par la Rédaction]

Introduction

Alpine freshwater systems are subject to anthropogenic disturbances, e.g., power dams (Petts 1984; The World Commission on Dams 2000; Petts and Gurnell 2005) and global warming (Xenopoulos et al. 2005; Buisson et al. 2008; Jonsson and Jonsson 2009). Fish can be used as a bioindicator of the health of freshwater sytems, and for that purpose freshwater ecologists have considered various variables indicative of fish populations, for instance abundance (number of fish per area unit of stream) (Heimbuch et al. 1997; Wyatt 2002), biomass (mass of fish per area unit of stream) and growth rate (Penczak et al. 1981), mortality rate (Gouraud et al. 2001), recruitment (Lobón-Cerviá 2009), or production (Kwak and Waters 1997).

Fish ecologists can use removal sampling by electrofishing to derive estimates of fish abundance (Lobón-Cerviá

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1991). Fish ecologists have created various Bayesian hierarchical models to statistically relate removal sampling data to abundance. The most simple model considers removal sampling data collected at a single stream section and bears on the assumption that catchability is equal among fish and across removals (Moran 1951; Cowx 1983; Bedrick 1994). This model has been popular among fish ecologists since the work of Carle and Strub (1978) who presented an algorithm to efficently compute a maximum likelihood estimate of the abundance. This approach actually provides inaccurate estimates of fish abundance (Riley and Fausch 1992; Peterson et al. 2004; Laplanche 2010). The main source of inaccuracy is unaccounted variability of the catchability or of the abundance. Several authors have therefore presented more advanced hierarchical models to estimate fish abundance from removal sampling data. Such models consider variability of the catchability between stream sections (Wyatt 2002, 2003), residual among fish (Dorazio et al. 2005; Mäntyniemi et al. 2005; Laplanche 2010), and variability of the abundance between stream sections (Wyatt 2002, 2003; Dorazio et al. 2008).

Catchability (Mahon 1980; Anderson 1995) and abundance (Pauly and Moreau 1997; Pitcher 2002) also fluctuate with fish length. The motivations to account for such variabilities within a Bayesian hierarchical model to derive abundance estimates are 3-fold. First, unaccounted variability of the catchability with fish length could lead to inaccurate abundance estimates. In the aim of providing accurate estimates, such a variability should be included (or at least its significance evaluated) within a removal sampling model. Second, the Bayesian approach makes possible the handling of complex mixed-effect, multilevel, nonlinear models (Congdon 2006). In this case, it is possible to consider multilevel, nonlinear length–catchability and length–abundance relationships. Variability of the abundance with fish length can be modeled as a mixture of distributions (Pauly and Moreau 1997; Pitcher 2002). Freshwater biologists usually decompose the length–abundance plots by using the method suggested by Bhattacharya (1967). Such a decomposition could be efficiently carried out within a Bayesian framework (Marin et al. 2005). Third, the description of the abundance as a function of fish length is the key to derive other variables indicative of fish populations, for instance growth rate (Pauly and Moreau 1997). Since weight plots from samples of fish populations show a well-pronounced linear relationship on a log–log scale (Cone 1989; Reiss 1989), i.e., fish weight is proportional to a power of fish length, biomass can be computed as the cross-product of the estimated abundance by the expected fish weight (Kwak and Waters 1997; (Lobón-Cerviá 2009).

We present a hierarchical Bayesian model that we use to estimate the abundance and the biomass of fish in an alpine stream by sampling at several stream sections. The model accounts for (*i*) variability of the abundance with fish length, (*ii*) random spatial variability of the abundance, (*iii*) variability of the catchability with fish length, (*iv*) random spatial variability of the catchability, and (*v*) residual variability of the catchability with fish. The data that is required to run the model is first described. The model is the combination of three submodels (abundance, weight, biomass) that are presented one after the other. We use the model with two datasets: a simulated dataset and a dataset collected in the field. We use the simulated dataset to compare parameter estimates with true values. We use the dataset collected in the field to illustrate the capability of the model to estimate the abundance and the biomass of brown trout in alpine streams. The model could be extended to estimate additional variables indicative of fish populations, such as growth rate, which is discussed.

Materials and methods

Measured variables

We consider s sections of a stream. Each stream section is depleted by electrofishing in r removals (Lobón-Cerviá 1991). Let A_h (m^2) be the area of the stream section $h \in \{1, \ldots, s\}$. Let $C_{h,j}$ be the number of fish caught during removal $j \in \{1, \ldots, r\}$ in section h and $C_h = \sum_{j=1}^{r} C_{h,j}$ be the total number of fish caught in section h. Let $L_{h,j,f}$ (mm) and $W_{h,j,f}$ (g) be the length and the weight of the fish $f \in \{1, \ldots, C_{hj}\}$ caught in section h during removal j. Fish are grouped by length class of width Δ_l (mm). The class width Δ_l can be equal to the measurement accuracy of the fish length (e.g., 1 mm) or larger. Let m be the number of length classes, $[(i-1)\Delta_l, i\Delta_l[$ the classes, and $L_i = (i - 1/2)\Delta_l$ the class centers ($i \in \{1, \ldots, m\}$). Let $C_{h,i,j}$ be the number of fish of length class i caught during removal j in section h. The measured variables considered in the following are A_h, $C_{h,i,j}$, L_i, $L_{h,j,f}$, and $W_{h,j,f}$ (Table 1).

Model structure

The model is structured in six hierarchical levels: stream (the all-embracing level), stream section ($h \in \{1, \ldots, s\}$), mixture component ($k \in \{1, \ldots, q\}$), length class ($i \in \{1, \ldots, m\}$), removal ($j \in \{1, \ldots, r\}$), and fish ($f \in \{1, \ldots, C_{h,j}\}$). The mixture component level (defined later) is part within the stream and section levels. Parameter notations are brought together (Table 1). Parameters at the stream (stream–component), section (section–component), length, and removal levels are of dimension 1 (q), s (sq), sm, and smr, respectively.

The model is the combination of three submodels (abundance, weight, and biomass) that are presented successively. The abundance and the biomass submodels are illustrated as directed acyclic graphs (DAG) (Figs. 1 and 2, respectively). The measured variables A_h, $C_{h,i,j}$, and L_i are used in the abundance submodel. The measured variables $L_{h,j,f}$ and $W_{h,j,f}$ are used in the weight submodel. The biomass submodel uses the measured variables A_h and L_i plus six variables (τ_k, $\tau_{h,k}$, $n_{h,i}$, c_h, d_h, s_h^2) of the abundance and weight submodels.

Abundance submodel

The submodel (Fig. 1) combines 22 mono- and multi-dimensional stochastic nodes: 13 at the stream level (λ, τ_k, μ_k, σ_k, a, b, η, π_λ, π_τ, π_μ, π_σ, π_a, π_b), 6 at the section level (λ_h, $\tau_{h,k}$, $\mu_{h,k}$, $\sigma_{h,k}$, a_h, b_h), 1 at the length level ($n_{h,i}$), and 1 at the removal level ($C_{h,i,j}$). The model comprehends 8 additional deterministic nodes: 1 at the stream level (λ_k), 2 at the section level (A_h, $\lambda_{h,k}$), 3 at the length level (L_i, $\lambda_{h,i}$, $\lambda_{h,i,k}$), and 2 at the removal level ($n_{h,i,j}$, $p_{h,i,j}$).

Table 1. Model parameters.

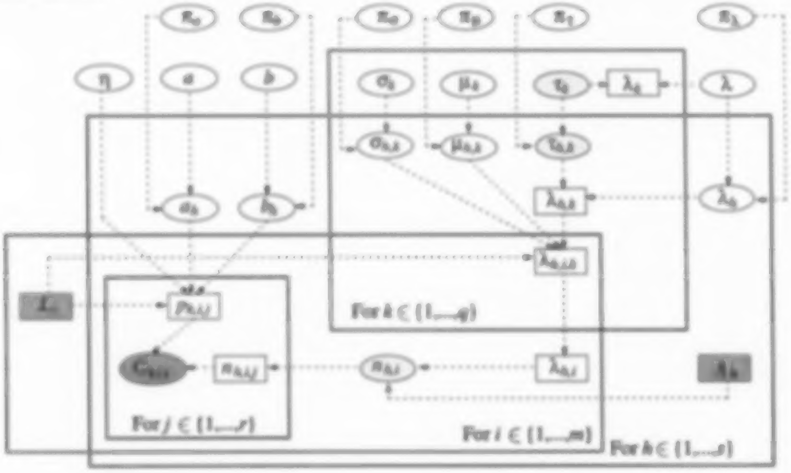
Parameter	Stream	Section	Size class	Component	Removal	Fish
Index	—	$h \in \{1, \ldots, s\}$	$i \in \{1, \ldots, m\}$	$k \in \{1, \ldots, q\}$	$j \in \{1, \ldots, r\}$	$f \in \{1, \ldots, n_{h,i,j}\}$
Measured variables[*]						
Area	—	A_h	—	—	—	—
Catch	—	C_h	$C_{h,i}$	—	$C_{h,i,j}$	—
Class center	—	—	L_i	—	—	—
Fish length	—	—	—	—	—	$L_{h,i,j,f}$
Fish weight	—	—	—	—	—	$W_{h,i,j,f}$
Abundance[†]						
Population size	—	n_h	$n_{h,i}$	—	$n_{h,i,j}$	—
Abundance	λ, λ_k	λ_h, $\lambda_{h,k}$	$\lambda_{h,i}$, $\lambda_{h,i,k}$	λ_k, $\lambda_{h,k}$, $\lambda_{h,i,k}$	—	—
Comp. proportion	τ_k	$\tau_{h,k}$	—	τ_k, $\tau_{h,k}$	—	—
Comp. center	μ_k	$\mu_{h,k}$	—	μ_k, $\mu_{h,k}$	—	—
Comp. bandwidth	σ_k	$\sigma_{h,k}$	—	σ_k, $\sigma_{h,k}$	—	—
Precisions	π_λ, π_τ, π_μ, π_σ	—	—	—	—	—
Catchability[†]						
Catchability	—	—	—	—	$p_{h,i,j}$	$p_{h,i,j,f}$
Slope, intercept	a, b	a_h, b_h	—	—	—	—
Variability	$1/\eta$	$1/\eta_h$	$1/\eta_{h,i}$	—	$1/\eta_{h,i,j}$	—
Precisions	π_a, π_b	—	—	—	—	—
Biomass[†]						
Allometric param.	c, d	c_h, d_h	—	—	—	—
Residual variance	s^2	s_h^2	—	—	—	—
Biomass	biom, biom$_k$	biom$_h$, biom$_{h,k}$	biom$_{h,i}$	biom$_k$, biom$_{h,k}$	—	—

Note: Parameters at the stream (stream-component), section (section-component), length, removal, and fish are of dimension 1 (q), s (sq), sm, smr, $smrn_{h,i,j}$, respectively.

[*] Measured variable.

[†] Latent variable.

Fig. 1. Directed acyclic graphs of the abundance submodel. Frames indicate hierarchical levels: section ($h \in \{1, \ldots, s\}$), length class ($i \in \{1, \ldots, m\}$), removal ($j \in \{1, \ldots, r\}$), and mixture component ($k \in \{1, \ldots, q\}$). Variables outside frames are variables at the stream hierarchical level. Rectangles, deterministic nodes; ellipses, stochastic nodes; dark filled nodes, observed variables; light filled nodes, output variables (τ_k, $\tau_{h,k}$, $n_{h,i}$) to the biomass submodel.

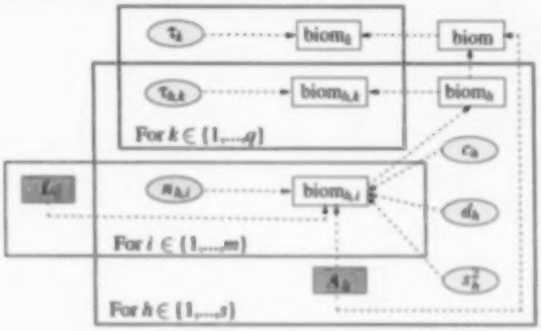


π_a
π_b
π_σ
π_μ
π_τ
π_λ
η
a
b
σ_k
μ_k
τ_k
λ_k
λ
$\sigma_{h,k}$
$\mu_{h,k}$
$\tau_{h,k}$
a_h
b_h
$\lambda_{h,k}$
λ_h
$\lambda_{h,i,k}$
L_i
$p_{h,i,j}$
For $k \in \{1,\ldots,q\}$
$C_{h,i,j}$
$n_{h,i,j}$
$n_{h,i}$
$\lambda_{h,i}$
A_h
For $j \in \{1,\ldots,r\}$
For $i \in \{1,\ldots,m\}$
For $h \in \{1,\ldots,s\}$

Removal sampling

Let $n_{h,i}$ be the number of fish of length class i in section h, and $n_{h,i,j}$ be the number of fish of length class i remaining in section h before removal j, i.e., $n_{h,i,1} = n_{h,i}$ and $n_{h,i,j} = n_{h,i,j-1} - C_{h,i,j-1}$ for $j \geq 2$. Let $p_{h,i,j}$ be the expectation of the catchability $p_{h,i,j,f}$ of the fish $f \in \{1, \ldots, n_{h,i,j}\}$ of length class

Fig. 2. Directed acyclic graphs of the biomass submodel. Hierarchical levels: section ($h \in \{1, \ldots, s\}$), length class ($i \in \{1, \ldots, m\}$), and mixture component ($k \in \{1, \ldots, q\}$). Light filled nodes, input variables (τ_k, $\tau_{h,k}$, $n_{h,i}$) from the abundance submodel and input variables (c_h, d_h, s_h) from the weight submodel.



i remaining in section h before removal j. Under several hypotheses (given later), the number of fish of length class i caught during removal j in section h is a binomial

$$(1) \qquad C_{h,i,j} | p_{h,i,j}, n_{h,i,j} \sim \text{Binomial}(p_{h,i,j}, n_{h,i,j}) \qquad \forall h, i, j$$

The modeling of the variability of the catchability $p_{h,i,j,f}$ (between length class, stream section, and residual) and of the population sizes $n_{h,i}$ (between length class and stream section) is detailed below.

Heterogeneity of the catchability between length class

We model variability of the catchability with fish length. To also model residual variability of the catchability between individuals of a same length class, we model variability with length of the expectation of the catchability during the first removal $p_{h,i,1}$. It is related to fish length by the logit regression model

$$(2) \qquad \text{logit}(p_{h,i,1}) = a_h L_i + b_h \qquad \forall h, i$$

The catchability $p_{h,i,1}$ increases with fish length if $a_h > 0$, decreases if $a_h < 0$, and does not vary with fish length if $a_h = 0$. The catchability $p_{h,i,1} = 1/2$ at the (algebraic) length $-b_h/a_h$.

Heterogeneity of the catchability within length class

We model residual individual variability of the catchability within a length class by assuming that the probabilities $p_{h,i,1,f}$ of capturing the fish $f \in \{1, \ldots, n_{h,i}\}$ (of length class i in section h) during the first removal are independent and beta distributed. We also assume that the probabilities of capturing any fish f during removal $j \geq 2$ given that the fish has not been captured earlier is equal to $p_{h,i,1,f}$. Under such hypotheses, Mäntyniemi et al. (2005) have shown that $p_{h,i,j,f}$ for $j \geq 2$ are still independent and beta distributed. As a result the number of caught fish $C_{h,i,j}$ is a binomial (hence eq. 1). Mäntyniemi et al. (2005) have shown that the expectation of $p_{h,i,j,f}$ is

$$(3) \qquad p_{h,i,j} = \frac{p_{h,i,1}}{1 + (j-1)/\eta_{h,i,1}} \qquad \forall h, i, j$$

where $p_{h,i,1} = \alpha_{h,i,1}/\eta_{h,i,1}$, $\eta_{h,i,1} = \alpha_{h,i,1} + \beta_{h,i,1}$, $\alpha_{h,i,1}$, and $\beta_{h,i,1}$ are the shape parameters of the beta distribution of $p_{h,i,1,f}$. For practical reasons, we parametrize the beta distribution of $p_{h,i,1,f}$ by using $p_{h,i,1}$ and $1/\eta_{h,i,1}$ instead of $\alpha_{h,i,1}$ and $\beta_{h,i,1}$. Indeed, $1/\eta_{h,i,1} = \delta_{h,i,1}/[p_{h,i,1}(1 - p_{h,i,1}) - \delta_{h,i,1}]$ where $\delta_{h,i,1}$ is the variance of $p_{h,i,1,f}$. $1/\eta_{h,i,1} = 0$ if there is no variability of the catchability between individuals. We assume in the following that the parameters $1/\eta_{h,i,1}$ are equal for all size classes and stream sections, hence $1/\eta_{h,i,1} = 1/\eta_h = 1/\eta$.

Table 2. Conditional distribution of the parameters at the section level.

Parameters
$\log(\lambda_h) \| \lambda, \pi_\lambda \sim \text{Normal}[\log(\lambda), \pi_\lambda]$
$\text{logit}(\tau'_{h,k}) \| \tau_k, \pi_\tau \sim \text{Normal}[\text{logit}(\tau_k), \pi_\tau]$
$\text{logit}\left(\frac{\mu_{h,k} - \mu^{\text{lim}}_{k-1}}{\mu^{\text{lim}}_k - \mu^{\text{lim}}_{k-1}}\right) \| \mu_k, \pi_\mu \sim \text{Normal}\left[\text{logit}\left(\frac{\mu_k - \mu^{\text{lim}}_{k-1}}{\mu^{\text{lim}}_k - \mu^{\text{lim}}_{k-1}}\right), \pi_\mu\right]$
$\log(\sigma_{h,k}) \| \sigma_k, \pi_\sigma \sim \text{Normal}[\log(\sigma_k), \pi_\sigma]$
$\log(a_h) \| a, \pi_a \sim \text{Normal}[\log(a), \pi_a]$
$\log(b_h) \| b, \pi_b \sim \text{Normal}[\log(b), \pi_b]$

Note: The mixture component proportions are $\tau_{h,k} = \tau'_{h,k} / \sum_{k'=1}^{q} \tau'_{h,k'}$ ($h \in \{1, \ldots, s\}$, $k \in \{1, \ldots, q\}$).

Size structure

The population sizes $n_{h,i}$ are taken to be independent Poisson random variables (Wyatt 2002)

$$(4) \qquad n_{h,i} | \lambda_{h,i}, A_h \sim \text{Poisson}(\lambda_{h,i} A_h)$$

where $\lambda_{h,i}$ and $\lambda_{h,i} A_h$ are the abundance and the expected number of fish of length class i in section h. We model variability of the abundance with fish length as a mixture of distributions (Pitcher 2002). We consider several distributions (Epanechnikov, biweight, triweight, and Gaussian) and denote K the respective kernels (Wand and Jones 1990). For instance, the Gaussian kernel is

$$(5) \qquad K(l) = \frac{1}{\sqrt{2\pi}} \exp\left(\frac{l^2}{2}\right) \qquad \forall l \in \mathbb{R}$$

The expected number of fish of length class i in section h is

$$(6) \qquad \lambda_{h,i} A_h = \lambda_h A_h \Delta_i \sum_{k=1}^{q} \frac{\tau_{h,k}}{\sigma_{h,k}} K\left(\frac{L_i - \mu_{h,k}}{\sigma_{h,k}}\right) \qquad \forall h, i$$

where λ_h and $\lambda_h A_h$ are the abundance and the expected number of fish in section h, q is the number of mixture components, $\mu_{h,k}$, $\sigma_{h,k}$, and $\tau_{h,k}$ ($k \in \{1, \ldots, q\}$) are the centers, the bandwiths, and the relative proportions of the mixture components, respectively. We also define $\lambda_{h,k} = \lambda_h \tau_{h,k}$ as the abundance of fish in section h of mixture component k. In the case of a Gaussian kernel, the centers and the bandwidths are expectations and standard deviations. The proportions are related by the constraint $\sum_{k=1}^{q} \tau_{h,k} = 1$ for all h. We sort the mixture components by increasing center, i.e., $\mu_{h,k} < \mu_{h,k+1}$ for all h and all $k \in \{1, \ldots, q-1\}$.

Variability among stream sections

We consider random variations among sections of the parameters related to the catchability (a_h, b_h) and the abundance (λ_h, $\tau_{h,k}$, $\mu_{h,k}$, $\sigma_{h,k}$). We provide additional expert

Table 1. Model parameters.

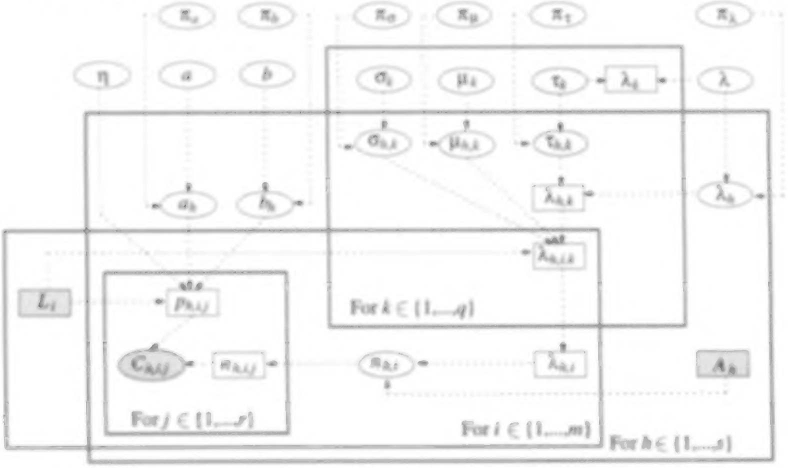
Parameter	Stream	Section	Size class	Component	Removal	Fish
Index	—	$h \in \{1, \ldots, s\}$	$i \in \{1, \ldots, m\}$	$k \in \{1, \ldots, q\}$	$j \in \{1, \ldots, r\}$	$f \in \{1, \ldots, n_{h,ij}\}$
Measured variables*						
Area	—	A_h	—	—	—	—
Catch	—	C_h	$C_{h,i}$	—	$C_{h,i,j}$	—
Class center	—	—	L_i	—	—	—
Fish length	—	—	—	—	—	$L_{h,i,j,f}$
Fish weight	—	—	—	—	—	$W_{h,i,j,f}$
Abundance†						
Population size	—	n_h	$n_{h,i}$	—	$n_{h,i,j}$	—
Abundance	λ, λ_k	λ_h, $\lambda_{h,k}$	$\lambda_{h,i}$, $\lambda_{h,i,k}$	λ_k, $\lambda_{h,k}$, $\lambda_{h,i,k}$	—	—
Comp. proportion	τ_k	$\tau_{h,k}$	—	τ_k, $\tau_{h,k}$	—	—
Comp. center	μ_k	$\mu_{h,k}$	—	μ_k, $\mu_{h,k}$	—	—
Comp. bandwidth	σ_k	$\sigma_{h,k}$	—	σ_k, $\sigma_{h,k}$	—	—
Precisions	π_λ, π_τ, π_μ, π_σ	—	—	—	—	—
Catchability†						
Catchability	—	—	—	—	$p_{h,i,j}$	$p_{h,i,j,f}$
Slope, intercept	a, b	a_h, b_h	—	—	—	—
Variability	$1/\eta$	$1/\eta_h$	$1/\eta_{h,i}$	—	$1/\eta_{h,i,j}$	—
Precisions	π_a, π_b	—	—	—	—	—
Biomass†						
Allometric param.	c, d	c_h, d_h	—	—	—	—
Residual variance	s^2	s_h^2	—	—	—	—
Biomass	biom, biom$_k$	biom$_h$, biom$_{h,k}$	biom$_{h,i}$	biom$_k$, biom$_{h,k}$	—	—

Note: Parameters at the stream (stream-component), section (section-component), length, removal, and fish are of dimension 1 (q), s (sq), sm, smr, $smrn_{h,i,j}$, respectively.

*Measured variable.

†Latent variable.

Fig. 1. Directed acyclic graphs of the abundance submodel. Frames indicate hierarchical levels: section ($h \in \{1, \ldots, s\}$), length class ($i \in \{1, \ldots, m\}$), removal ($j \in \{1, \ldots, r\}$), and mixture component ($k \in \{1, \ldots, q\}$). Variables outside frames are variables at the stream hierarchical level. Rectangles, deterministic nodes; ellipses, stochastic nodes; dark filled nodes, observed variables; light filled nodes, output variables (τ_k, $\tau_{h,k}$, $n_{h,i}$) to the biomass submodel.


π_a
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$\lambda_{h,k}$
λ_h
$\lambda_{h,i,k}$
L_i
$p_{h,i,j}$
For $k \in \{1,\ldots,q\}$
$C_{h,i,j}$
$n_{h,i,j}$
$n_{h,i}$
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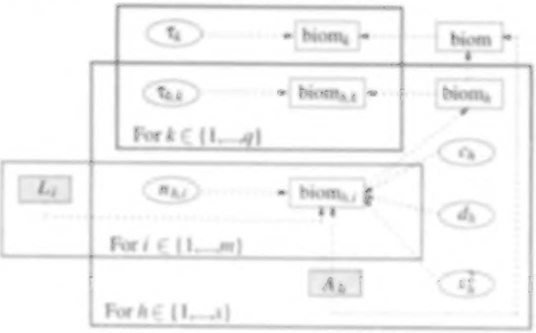
Removal sampling

Let $n_{h,i}$ be the number of fish of length class i in section h, and $n_{h,i,j}$ be the number of fish of length class i remaining in section h before removal j, i.e., $n_{h,i,1} = n_{h,i}$ and $n_{h,i,j} = n_{h,i,j-1} - C_{h,i,j-1}$ for $j \geq 2$. Let $p_{h,i,j}$ be the expectation of the catchability $p_{h,i,j,f}$ of the fish $f \in \{1, \ldots, n_{h,i,j}\}$ of length class

Fig. 2. Directed acyclic graphs of the biomass submodel. Hierarchical levels: section ($h \in \{1, \ldots, s\}$), length class ($i \in \{1, \ldots, m\}$), and mixture component ($k \in \{1, \ldots, q\}$). Light filled nodes, input variables (τ_k, $\tau_{h,k}$, $n_{h,i}$) from the abundance submodel and input variables (c_h, d_h, s_h) from the weight submodel.



i remaining in section h before removal j. Under several hypotheses (given later), the number of fish of length class i caught during removal j in section h is a binomial

$$(1) \quad C_{h,i,j} | p_{h,i,j}, n_{h,i,j} \sim \text{Binomial}(p_{h,i,j}, n_{h,i,j}) \qquad \forall h, i, j$$

The modeling of the variability of the catchability $p_{h,i,j,f}$ (between length class, stream section, and residual) and of the population sizes $n_{h,i}$ (between length class and stream section) is detailed below.

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We model residual individual variability of the catchability within a length class by assuming that the probabilities $p_{h,i,1,f}$ of capturing the fish $f \in \{1, \ldots, n_{h,i}\}$ (of length class i in section h) during the first removal are independent and beta distributed. We also assume that the probabilities of capturing any fish f during removal $j \geq 2$ given that the fish has not been captured earlier is equal to $p_{h,i,1,f}$. Under such hypotheses, Mäntyniemi et al. (2005) have shown that $p_{h,i,j,f}$ for $j \geq 2$ are still independent and beta distributed. As a result the number of caught fish $C_{h,i,j}$ is a binomial (hence eq. 1). Mäntyniemi et al. (2005) have shown that the expectation of $p_{h,i,j,f}$ is

$$(3) \quad p_{h,i,j} = \frac{p_{h,i,1}}{1 + (j-1)/\eta_{h,i,1}} \qquad \forall h, i, j$$

where $p_{h,i,1} = \alpha_{h,i,1}/\eta_{h,i,1}$, $\eta_{h,i,1} = \alpha_{h,i,1} + \beta_{h,i,1}$, $\alpha_{h,i,1}$, and $\beta_{h,i,1}$ are the shape parameters of the beta distribution of $p_{h,i,1,f}$. For practical reasons, we parametrize the beta distribution of $p_{h,i,1,f}$ by using $p_{h,i,1}$ and $1/\eta_{h,i,1}$ instead of $\alpha_{h,i,1}$ and $\beta_{h,i,1}$. Indeed, $1/\eta_{h,i,1} = \delta_{h,i,1} / [p_{h,i,1} (1 - p_{h,i,1}) - \delta_{h,i,1}]$ where $\delta_{h,i,1}$ is the variance of $p_{h,i,1,f}$. $1/\eta_{h,i,1} = 0$ if there is no variability of the catchability between individuals. We assume in the following that the parameters $1/\eta_{h,i,1}$ are equal for all size classes and stream sections, hence $1/\eta_{h,i,1} = 1/\eta_h = 1/\eta$.

Table 2. Conditional distribution of the parameters at the section level.

Parameters
$\log(\lambda_h) \vert \lambda, \pi_\lambda \sim \text{Normal}\,[\log(\lambda), \pi_\lambda]$
$\text{logit}(\tau'_{h,k}) \vert \tau_k, \pi_\tau \sim \text{Normal}\,[\text{logit}(\tau_k), \pi_\tau]$
$\text{logit}\left(\frac{\mu_{h,k} - \mu_{k-1}^{\lim}}{\mu_k^{\lim} - \mu_{k-1}^{\lim}}\right) \vert \mu_k, \pi_\mu \sim \text{Normal}\left[\text{logit}\left(\frac{\mu_k - \mu_{k-1}^{\lim}}{\mu_k^{\lim} - \mu_{k-1}^{\lim}}\right), \pi_\mu\right]$
$\log(\sigma_{h,k}) \vert \sigma_k, \pi_\sigma \sim \text{Normal}[\log(\sigma_k), \pi_\sigma]$
$\log(a_h) \vert a, \pi_a \sim \text{Normal}[\log(a), \pi_a]$
$\log(b_h) \vert b, \pi_b \sim \text{Normal}[\log(b), \pi_b]$

Note: The mixture component proportions are $\tau_{h,k} = \tau'_{h,k} / \sum_{l=1}^{q} \tau'_{h,l}$, ($h \in \{1, \ldots, s\}$, $k \in \{1, \ldots, q\}$).

Size structure

The population sizes $n_{h,i}$ are taken to be independent Poisson random variables (Wyatt 2002)

$$(4) \quad n_{h,i} | \lambda_{h,i}, A_h \sim \text{Poisson}(\lambda_{h,i} A_h)$$

where $\lambda_{h,i}$ and $\lambda_{h,i} A_h$ are the abundance and the expected number of fish of length class i in section h. We model variability of the abundance with fish length as a mixture of distributions (Pitcher 2002). We consider several distributions (Epanechnikov, biweight, triweight, and Gaussian) and denote K the respective kernels (Wand and Jones 1990). For instance, the Gaussian kernel is

$$(5) \quad K(l) = \frac{1}{\sqrt{2\pi}} \exp\left(\frac{l^2}{2}\right) \qquad \forall l \in \mathbb{R}$$

The expected number of fish of length class i in section h is

$$(6) \quad \lambda_{h,i} A_h = \lambda_h A_h \Delta_i \sum_{k=1}^{q} \frac{\tau_{h,k}}{\sigma_{h,k}} K\left(\frac{L_i - \mu_{h,k}}{\sigma_{h,k}}\right) \qquad \forall h, i$$

where λ_h and $\lambda_h A_h$ are the abundance and the expected number of fish in section h, q is the number of mixture components, $\mu_{h,k}$, $\sigma_{h,k}$, and $\tau_{h,k}$ ($k \in \{1, \ldots, q\}$) are the centers, the bandwiths, and the relative proportions of the mixture components, respectively. We also define $\lambda_{h,k} = \lambda_h \tau_{h,k}$ as the abundance of fish in section h of mixture component k. In the case of a Gaussian kernel, the centers and the bandwidths are expectations and standard deviations. The proportions are related by the constraint $\sum_{k=1}^{q} \tau_{h,k} = 1$ for all h. We sort the mixture components by increasing center, i.e., $\mu_{h,k} < \mu_{h,k+1}$ for all h and all $k \in \{1, \ldots, q-1\}$.

Variability among stream sections

We consider random variations among sections of the parameters related to the catchability (a_h, b_h) and the abundance (λ_h, $\tau_{h,k}$, $\mu_{h,k}$, $\sigma_{h,k}$). We provide additional expert

Table 3. Free parameters (stream level) are assigned vague priors.

Parameter	Prior	Marginal posterior
λ	Gamma(0.001, 0.001)	Lognormal(–0.35, 4)
τ'_k	Uniform(0,1)	Beta([27, 21, 11], [35, 39, 38])
μ_k	Uniform(μ^{lim}_{k-1}, μ^{lim}_k)	Normal([53, 121, 188], [0.1, 0.3, 0.03)]
σ^2_k	InvGamma(0.001, 0.001)	Lognormal([3.9, 5.4, 6.9], [37, 29, 15])
a	Normal(0, 0.001)	Normal(7.6, 0.14)
b	Normal(0, 0.001)	Normal(0.44, 6.6)
$1/\eta$	InvGamma(0.001, 0.001)	Beta(0.2, 1.4)
π_λ	Gamma(0.001, 0.001)	Gamma(0.9, 0.09)
π_τ	Gamma(0.001, 0.001)	Gamma(1.2, 0.25)
π_μ	Gamma(0.001, 0.001)	Gamma(2.0, 0.06)
π_σ	Gamma(0.001, 0.001)	Gamma(0.4, 0002)
π_a	Gamma(0.001, 0.001)	Gamma(0.1, 0.001)
π_b	Gamma(0.001, 0.001)	Gamma(0.3, 0.001)

Note: Parameters are shape and rate for gamma distributions, expectation and precision for normal and lognormal distributions, and shapes for β-distributions. The mixture component proportions are $\tau_k = \tau'_k / \sum_{k'=1}^{q} \tau'_{k'}$ ($k \in \{1, \ldots, q\}$). The last column provides the approximate distribution of the marginal posteriors of the free parameters (values within brakets refer to the first, second, and third mixture components, respectively) by using model alternative 1 with the Neste d'Oueil dataset.

knowledge that the definition sets of the mixture component centers do not overlap and have boundaries common for all sections. As a result, we add the constraints $\mu^{\text{lim}}_{k-1} < \mu_{h,k} < \mu^{\text{lim}}_k$ for all section h and mixture component k, with $\mu^{\text{lim}}_0 = 0$. The parameters at the section level are therefore bound to the constraints: $0 < \lambda_h$, $0 < \tau_{h,k} < 1$ with $\sum_{k=1}^{q} \tau_{h,k} = 1$, $\mu^{\text{lim}}_{k-1} < \mu_{h,k} < \mu^{\text{lim}}_k$, $0 < \sigma_{h,k}$. We log-transform, scale, and logit-transform the above parameters and assign normal distributions of expectations the respective values at the stream level (Table 2). We label π_λ, π_τ, π_μ, π_σ, π_a, π_b the precisions (i.e., the inverse of the variances) of the normal distributions. We assume that the precisions of the normal distributions related to $\tau_{h,k}$, $\mu_{h,k}$, and $\sigma_{h,k}$ are equal for all k.

Priors

The free parameters are λ, τ_k, μ_k, σ_k, a, b, η, and the precisions π_λ, π_τ, π_μ, π_σ, π_a, π_b. We apply the constraints $\mu^{\text{lim}}_{k-1} < \mu_k < \mu^{\text{lim}}_k$ on the mixture component centers. We assign vague priors to all free parameters (Table 3). The abundance of fish of mixture component k is $\lambda_k = \lambda\tau_k$.

Weight submodel

We relate the weight and the length of the fish $f \in \{1, \ldots, C_{h,j}\}$ caught during removal j in section h by the allometric relationship

$$(7) \qquad W_{h,j,f} = c_h L_{h,j,f}^{d_h} \exp(\epsilon_{h,j,f}) \quad \forall h, j, f$$

with $c_h | c, \pi_c \sim \text{Normal}(c, \pi_c)$ and $d_h | d, \pi_d \sim \text{Normal}(d, \pi_d)$, i.e., over- or under-weight of fish is allowed to vary between stream sections. The error in eq. 7 is lognormal, $\epsilon_{h,j,f} | s^2_h \sim \text{Normal}(0, 1/s^2_h)$. The error terms $c_h - c | \pi_c$, $d_h - d | \pi_d$, and $\epsilon_{h,j,f} | s^2_h$ are taken independent. Log-transformed, the weight submodel is a two-level linear mixed-effect model with a normal, heteroscedastic residual error (Pinheiro and Bates 2000).

The weight submodel that has just been described applies to a subset of C_h fish among the n_h fish present in section h. We assume that the fish used for model selection and parameter estimation are representative, in terms of length and weight, of the fish present in section h. In that case, the weight of the fish $f \in \{1, \ldots, n_h\}$ of section h are provided by the same weight submodel.

Biomass submodel

The biomass $\text{biom}_{h,i}$ of fish of length class i in section h is

$$(8) \qquad \text{biom}_{h,i} = \sum_{j=1}^{r} \sum_{f=1}^{n_{h,i}} W_{h,i,f} / A_h \quad \forall h, i$$

which is approximately equal to eq. 9 (as shown in Appendix A and discussed later)

$$(9) \qquad \text{biom}_{h,i} = n_{h,i} c_h L_i^{d_h} \exp(s^2_h/2) / A_h \quad \forall h, i$$

The biomass of fish in section h is

$$(10) \qquad \text{biom}_h = \sum_{i=1}^{m} \text{biom}_{h,i} \quad \forall h$$

The average biomass of fish (stream level) is

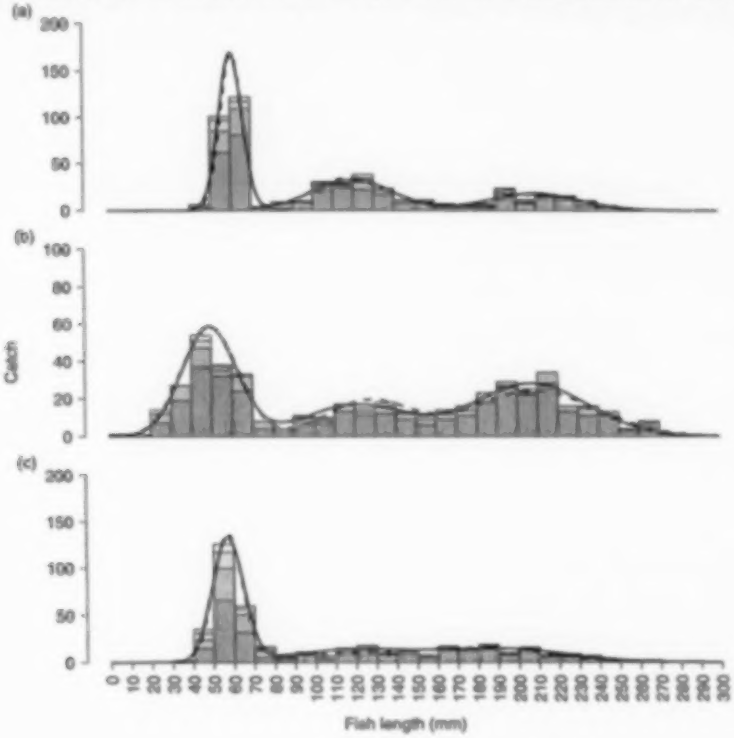
$$(11) \qquad \text{biom} = \sum_{h=1}^{s} \text{biom}_h A_h \Big/ \sum_{h=1}^{s} A_h$$

and the biomass of fish in mixture component k is $\text{biom}_k = \tau_k \text{biom}$. The relationship between the biomass variables, the measured variables (A_h, L_i), and the input variables from the abundance submodel (τ_k, $\tau_{h,k}$, $n_{h,i}$) and from the weight submodel (c_h, d_h, s^2_h) are illustrated by a DAG (Fig. 2).

Computations

Computations of the three submodels can be carried out simultaneously by merging the submodels into a single hierarchical model. Computations of the three submodels can also be carried out successively. We chose to first carry out

Fig. 3. Number of caught fish $C_{h,i,j}$ per Δ_l = 10 mm length class (simulated dataset). The catch $C_{h,i,j}$ is the *j*th stacked sub-bar making up the bar of *i*th length class (*x*-axis) of the *h*th subplot. The true (broken line) and estimated (unbroken line) value of the expected population sizes $\lambda_{h,i}A_h\Delta_l$ are computed by using eq. 6 with the true value and the point estimates of the parameters λ_h, $\tau_{h,k}$, $\mu_{h,k}$, and $\sigma_{h,k}$ (Table 6).



the computations related to the weight submodel, before jointly carring out the computations related to the abundance and biomass submodels (referred to in the following as the abundance–biomass model).

Models have been implemented by using OpenBUGS, open source version of WinBUGS (Lunn et al. 2009; Ntzoufras 2009). Computations of the weight submodel could, however, have been carried out by using R (Pinheiro and Bates 2000). Samples of the posterior are generated by using a Markov chain Monte Carlo (MCMC) method (Robert and Casella 2004). Samples are processed by using R (Crawley 2007). WinBUGS and R scripts are, together with data files, available online in the supplementary data[2], see Appendix S1. Reported point estimates of the parameters are posterior expectation estimates. Interval estimates are 2.5% and 97.5% quantile estimates of marginal posteriors. Convergence was investigated by using the ANOVA-type diagnostic described by Gelman and Rubin (1992) with three chains. Independent samples were obtained by thinning, guided through the examination of the autocorrelation functions of the posterior samples. One thousand independent posterior samples were generated for each model.

Alternative models are compared in terms of the Deviance Information Criterion, DIC = $\bar{D} + p_D$, where $\bar{D}$ is the posterior expectation of the deviance statistics and p_D is a count of effective parameters (Spiegelhalter et al. 2002). Weight submodel alternatives are compared by using the DIC routine provided by OpenBUGS. The computation of the DIC is, however, not straightforward when using discrete variables. The conditional distribution of $C_{h,i,j}$ is discrete (binomial), for that reason we have not compared abundance–biomass models by using the DIC routine provided by OpenBUGS. We have computed approximate DIC estimates by approximating the count of effective parameters p_D by the true number of parameters.

Datasets

Simulated dataset

We simulate a removal sampling dataset ($s = 3$, $m = 299$, $r = 4$, $q = 3$ Gaussian components, $\Delta_l = 1$ mm). The areas of the stream sections are $A_1 = A_2 = A_3 = 500$ m^2. We set the values of the free parameters (stream level) to simulate parameter values at the section, length, and removal levels. The weight of the fish are simulated by using the weight submodel with parameter values found by using the field dataset (described below). The number of caught fish are C_1 = 496, C_2 = 474, and C_3 = 434. The number of caught fish $C_{h,i,j}$, as well as the true value of the expected population sizes $\lambda_{h,i}A_h\Delta_l$, are illustrated by a length–abundance plot (Fig. 3).

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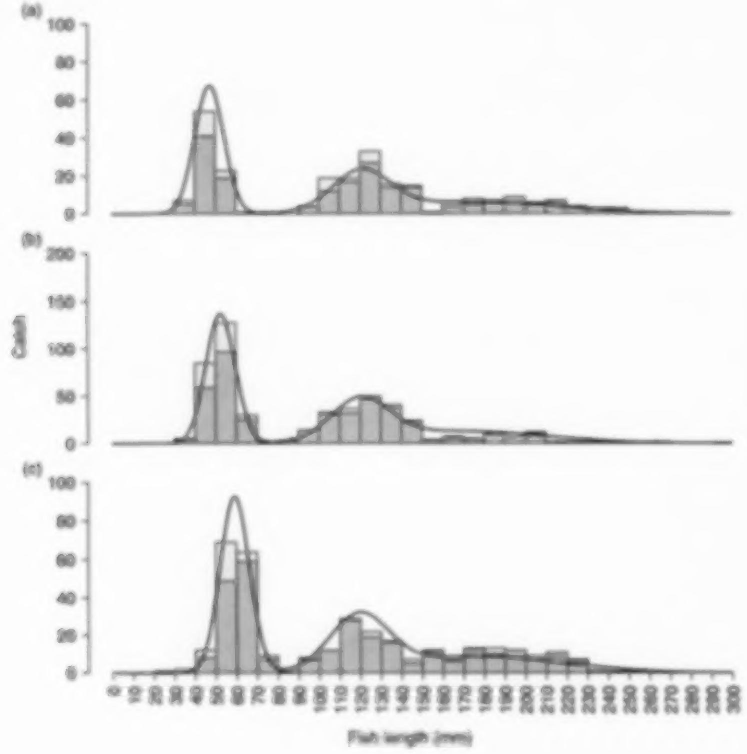
[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

Table 4. Abundance point estimates (section level) by using the simulated dataset with $r \in \{2, 3, 4\}$ removals and length class widths $\Delta_l \in \{1, 2, 5, 10, 20\}$ mm.

	$r = 2$			$r = 3$			$r = 4$		
Δ_l	$\hat{\lambda}_1$	$\hat{\lambda}_2$	$\hat{\lambda}_3$	$\hat{\lambda}_1$	$\hat{\lambda}_2$	$\hat{\lambda}_3$	$\hat{\lambda}_1$	$\hat{\lambda}_2$	$\hat{\lambda}_3$
1	1.02	1.01	0.94	1.00	0.97	0.94	1.01	0.97	0.95
2	1.04	1.02	0.96	1.01	0.97	0.94	1.01	0.97	0.95
5	1.05	1.04	0.97	1.01	0.97	0.94	1.01	0.97	0.95
10	1.04	1.02	0.97	1.01	0.97	0.94	1.01	0.97	0.95
20	1.04	1.00	0.96	1.03	0.97	0.95	1.04	0.97	0.97

Note: True values are $\lambda_1 = 0.98$, $\lambda_2 = 0.97$, and $\lambda_3 = 0.87$ fish/m^2.

Fig. 4. Number of caught fish $C_{h,l,j}$ per $\Delta_l = 10$ mm length class at the Neste d'Oueil in July 2006 at Cires (*a*), Mayrègne (*b*), and Saint-Paul (*c*). The estimated expected population sizes (solid curve) is computed by using eq. 6 with the point estimates of the parameters λ_h, $\pi_{h,k}$, $\mu_{h,k}$, and $\sigma_{h,k}$ (Table 8).



We investigate the consequences of degrading the information brought by the data by lowering the number of removals and enlarging the length class width. For that purpose, we reduce the original $\Delta_l = 1$ mm, 4-removal sampling dataset into 14 additionnal datasets ($r \in \{2, 3, 4\}$, $\Delta_l \in \{1, 2, 5, 10, 20\}$ mm, Table 4).

Field dataset

Data were collected in July 2006 at three locations on the Neste d'Oueil stream (Haute-Garonne, Pyrénées mountain range, France): Cires ($h = 1$), Mayrègne ($h = 2$), and Saint-Paul ($h = 3$). Stream sections are described elsewhere (Laplanche 2010). The stream has been electrofished in $r = 2$ removals. Only brown trout (*Salmo trutta fario*) are considered (Klemetsen et al. 2003). The number of caught fish per 10 mm length class are illustrated by a length–abundance plot (Fig. 4). The total number of fish caught are $C_1 = 246$, $C_2 = 509$, and $C_3 = 341$, respectively. We weighed only a fraction of the caught fish in July 2006. The weight dataset was enlarged by using fish caught in October 2006, leading to 133, 271, and 132 weight measurements at Cires, Mayrègne, and Saint-Paul, respectively.

Results

Length–weight relationship

Seven model reductions are considered, depending which constraints among $c_k = c$, $d_k = d$, and $s_k^2 = s^2$ are considered

Table 5. Weight submodel reductions and respective DIC.

Alternative	$c_h = c$	$d_h = d$	$s_h^2 = s^2$	DIC
1	–	–	–	2552
2	*x*	–	–	2551
3	–	*x*	–	2552
4	*x*	*x*	–	2619
5	–	–	*x*	2552
6	*x*	–	*x*	2551
7	–	*x*	*x*	2551
8	*x*	*x*	*x*	2617

Note: Alternative 1 is the model of eq. 7 with variability among stream sections of the parameters c_h, d_h, and s_h^2. Alternative 8 is the most reduced model, by assuming that the parameters c_h, d_h, and s_h^2 are equal for all sections; *x*, constrained; –, not constrained.

(Table 5). Burn-in (2500 iterations) and thinning (500) was investigated by using the most expanded model (alternative 1). The DIC estimates of the alternative weight submodels are also provided (Table 5). Alternative models can be classified into two groups: Models 4 and 8 of high DIC $\in$ {2617, 2619} and remaining models (1–3, 5–7) of lower DIC $\in$ {2551, 2552}. DIC results suggest that variability of c_h and (or) d_h should be considered, by rejecting models 4 and 8. Results also suggest that it is not relevant to include variability among sections of the residual variance in the weight submodel, in favor of models 5–7. Given that DIC results cannot discriminate among the remaining alternative models, we choose the most expanded model 5, i.e., model of eq. 7 with homoscedastistic residual error. Point (and interval) parameter estimates are $\widehat{c}_1 = 6.42$ (4.93, 8.08), $\widehat{c}_2 = 8.65$ (7.36, 10.19), $\widehat{c}_3 = 7.77$ (6.35, 9.34) μg/mm³ and $\widehat{d}_1 = 3.088$ (3.041, 3.138), $\widehat{d}_2 = 3.030$ (2.997, 3.062), $\widehat{d}_3 = 3.063$ (3.025, 3.102) at Cires, Mayrègne, and Saint-Paul, respectively. The residual variance is $\widehat{s}^2 = 0.0047$ (0.0042, 0.0053).

Simulated dataset

Abundance is estimated by using the 4-removal, 3-removal, and 2-removal simulated dataset with $\Delta_l \in \{1, 2, 5, 10, 20\}$ mm (Table 4). It is not possible to use an index of complexity and fit to select the number of removals or the length class width, since the measured variables of models with different number of removals or class widths are distinct. Results show that, in the case of this dataset, abundance point estimates are not sensitive to the choice of the width of the length class, given that the width is small enough ($\Delta_l \leq 10$ mm). This result also applies to the remaining parameters as well as interval estimates (available online in Supplemental Appendix S1). Given that processing is faster (approximately 2, 5, 10, and 20× as fast) by using larger widths ($\Delta_l \in \{2, 5, 10, 20\}$ mm), following computations are carried out by using a $\Delta_l = 10$ mm class width. Results also show that the degradation of the information by using 3 removals is in this case negligible. Point and interval estimates of the parameters at the stream and section levels by using the 2-removal dataset with $\Delta_l = 10$ mm are provided (Burn-in: 50 000, thinning: 500) (Table 6). The estimated expected population sizes $\lambda_h A_h \Delta_l$ are illustrated (Fig. 3).

Field dataset

Fifteen abundance-biomass model alternatives are considered (Table 7). The first alternative (baseline model) is the abundance–biomass model that has been previously described with $q = 3$ Gaussian components ($\mu_1^{\text{lim}} = 100$, $\mu_2^{\text{lim}} = 150$, $\mu_3^{\text{lim}} = 250$ mm). The second alternative (as well as the remaining alternatives) do not consider residual variability among fish of the catchability. In that case, $1/\eta = 0$ and eq. 3 simplifies into $p_{h,l,j} = p_{h,l,1}$, i.e., catchability is constant across removals. The third alternative describes the size structure as a mixture of triweight kernels, $K(l) = (35/32)(1 - l^2)^3$ for $l \in [-1, 1]$ and $K(l) = 0$ elsewhere. The fourth alternative describes the size structure as a mixture of $q = 4$ Gaussian components. In that case the boundaries of the mixture component centers are $\mu_1^{\text{lim}} = 100$, $\mu_2^{\text{lim}} = 150$, $\mu_3^{\text{lim}} = 200$, and $\mu_4^{\text{lim}} = 250$ mm. The remaining alternatives are model reductions that do not consider variability of the catchability with fish length (in that case $a_h = a = 0$ and eq. 2 becomes $\text{logit}(p_{h,l,1}) = b_h$) and (or) do not consider variability among stream sections of the parameters λ_h, $\tau_{h,k}$, $\mu_{h,k}$, $\sigma_{h,k}$, a_h, and b_h. Deviance, complexity, and DIC of model alternatives 2–15 are compared with respective values of the baseline model (Table 7). Burn-in (5000) and thinning (100) for alternative 2 were used for alternatives 3–15. Computations of the most expanded model (alternative 1) required larger burn-in (50 000) and thinning (500).

Results suggest that, in this case study, residual variability among fish of the catchability is not significant (by comparing alternatives 1, 2), the use of the Gaussian or triweight kernel are comparable (2, 3), and the use of 4 Gaussian components is ill-advised (2, 4). Results suggest that it is not relevant to consider variability among locations of a_h, b_h, $\tau_{h,k}$, $\sigma_{h,k}$ (2, 7, 9, 10). Results strongly suggest that variability with fish length of the catchability and variability among locations of λ_h and $\mu_{h,k}$ should be considered (2, 5, 6, 8). Remaining results (11, 12, 13, 14, 15) are in favor of model alternative 12, i.e., the abundance submodel described earlier with $q = 3$ Gaussian components without variability among locations of a_h, b_h, $\tau_{h,k}$, $\sigma_{h,k}$ nor residual variability of the catchability.

Point and interval estimates of the parameters at the stream and section levels are computed by using model alternative 12 (Table 8). The estimated abundances at Cires, Mayrègne, Saint-Paul (section level) and the Neste d'Oueil (stream level) are $\widehat{\lambda}_1 = 0.53$, $\widehat{\lambda}_2 = 0.98$, $\widehat{\lambda}_3 = 0.62$, and $\widehat{\lambda} = 0.83$ fish/m², respectively. The estimated biomasses are 11.50, 19.88, 14.76, and 15.47 g/m², respectively. Estimated expected population sizes are represented together with $C_{h,l,j}$ (Fig. 4).

Discussion

Point (and interval) estimates of the abundance of 0+ trout parrs at Cires, Mayrègne, and Saint-Paul are $\widehat{\lambda}_{1,1} = 0.24$ (0.21,0.28), $\widehat{\lambda}_{2,1} = 0.45$ (0.40,0.50), $\widehat{\lambda}_{3,1} = 0.29$ (0.25,0.32) fish/m². These results are similar to those found by Laplanche (2010): $\widehat{\lambda}_{1,1} = 0.18$ (0.15,0.24), $\widehat{\lambda}_{2,1} = 0.49$ (0.45,0.58), $\widehat{\lambda}_{3,1} = 0.29$ (0.26,0.36) fish/m². Laplanche (2010) presented a hierarchical model accounting for ran-

Table 6. True value and parameter estimates (stream and section levels) by using the simulated data-set with $r = 2$ removals and a $\Delta_l = 10$ mm class width.

Unit	Parameter	$q_{2.5\%}$	Truth	Estimate	$q_{97.5\%}$
—	$1/\eta$	0.00	0.10	0.11	0.66
—	π_a	0.0	10	122.5	1068.0
—	π_b	0.2	10	79.3	707.3
—	π_τ	4.5	50	350.4	1746.0
—	π_μ	1.9	10	16.6	60.2
—	π_σ	1.8	10	10.0	26.5
—	π_λ	0.5	10	4.2	13.7
g/m^2	biom	29.53	31.63	31.34	37.74
Fish/m^2	λ	0.80	1	1.02	1.46
—	τ_1	0.32	0.50	0.45	0.58
—	τ_2	0.16	0.30	0.27	0.40
—	τ_3	0.16	0.20	0.28	0.41
mm	μ_1	44.7	50	55.2	64.9
mm	μ_2	113.5	125	120.4	127.6
mm	μ_3	191.3	200	203.6	214.0
mm	σ_1	5.2	10	8.5	13.1
mm	σ_2	15.6	20	26.6	43.8
mm	σ_3	16.1	30	27.3	42.9
—	b	−1.25	0	−0.17	0.74
Per metre	10^3a	2.8	5	6.7	10.8
g/m^2	biom$_1$	25.1	26.8	26.9	32.8
Fish/m^2	λ_1	0.90	0.98	1.04	1.47
—	$\tau_{1,1}$	0.43	0.44	0.48	0.55
—	$\tau_{1,2}$	0.27	0.32	0.32	0.37
—	$\tau_{1,3}$	0.15	0.18	0.20	0.24
mm	$\mu_{1,1}$	59.4	60.7	60.2	61.0
mm	$\mu_{1,2}$	116.4	119.4	120.0	123.6
mm	$\mu_{1,3}$	203.2	209.0	209.3	214.5
mm	$\sigma_{1,1}$	5.1	5.4	5.7	6.4
mm	$\sigma_{1,2}$	17.0	18.9	20.1	23.8
mm	$\sigma_{1,3}$	18.1	22.4	22.3	27.4
—	b_1	−1.06	0.01	−0.07	0.56
Per metre	10^3a_1	2.5	4.9	6.4	10.2
g/m^2	biom$_2$	41.33	43.83	43.59	51.35
Fish/m^2	λ_2	0.89	0.97	1.02	1.43
—	$\tau_{2,1}$	0.33	0.43	0.40	0.47
—	$\tau_{2,2}$	0.15	0.21	0.22	0.31
—	$\tau_{2,3}$	0.30	0.39	0.39	0.46
mm	$\mu_{2,1}$	46.5	49.1	48.9	51.3
mm	$\mu_{2,2}$	113.7	126.8	121.1	129.0
mm	$\mu_{2,3}$	200.3	208.4	206.7	212.7
mm	$\sigma_{2,1}$	11.7	13.8	13.3	15.3
mm	$\sigma_{2,2}$	17.6	20.8	26.6	43.8
mm	$\sigma_{2,3}$	23.9	30.5	28.1	32.9
—	b_2	−1.02	0.44	0.01	0.70
Per metre	10^3a_2	3.3	4.7	6.7	10.3
g/m^2	biom$_3$	21.2	24.3	23.5	30.1
Fish/m^2	λ_3	0.80	0.87	0.97	1.38
—	$\tau_{3,1}$	0.47	0.45	0.54	0.61
—	$\tau_{3,2}$	0.15	0.20	0.25	0.35
—	$\tau_{3,3}$	0.14	0.17	0.22	0.30
mm	$\mu_{3,1}$	55.8	56.9	56.9	58.2
mm	$\mu_{3,2}$	110.2	125.4	119.9	129.6
mm	$\mu_{3,3}$	182.5	189.9	194.9	205.9
mm	$\sigma_{3,1}$	6.5	7.1	7.6	8.7
mm	$\sigma_{3,2}$	20.0	42.0	33.3	48.2
mm	$\sigma_{3,3}$	24.3	30.4	30.4	38.4
—	b_3	−1.31	−0.11	−0.45	0.20
Per metre	10^3a_3	3.4	4.8	7.1	12.0

Note: —, no unit.

Table 7. Abundance submodel alternatives, estimated deviances, and differences of complexity and DIC to the baseline model (alternative 1) by using the field dataset.

Alternative	Kernel	q	$1/\eta = 0$	$a_h = a = 0$	$\lambda_h = \lambda$	$\tau_{h,k} = \tau_k$	$\mu_{h,k} = \mu_k$	$\sigma_{h,k} = \sigma_k$	$a_h = a$, $b_h = b$	$\bar{D}$	Δp	ΔDIC
1	Gaussian	3	–	–	–	–	–	–	–	343.3	0	0
2	Gaussian	3	x	–	–	–	–	–	–	321.9	–1	–22.4
3	Triweight	3	x	–	–	–	–	–	–	323.2	–1	–21.1
4	Gaussian	4	x	–	–	–	–	–	–	321.2	+8	–14.1
5	Gaussian	3	x	x	–	–	–	–	–	354.5	–4	+7.2
6	Gaussian	3	x	–	x	–	–	–	–	367.5	–3	+21.2
7	Gaussian	3	x	–	–	x	–	–	–	323.8	–5	–24.5
8	Gaussian	3	x	–	–	–	x	–	–	337.5	–7	–12.8
9	Gaussian	3	x	–	–	–	–	x	–	322.1	–7	–28.2
10	Gaussian	3	x	–	–	–	–	–	x	320.7	–5	–27.6
11	Gaussian	3	x	–	–	x	–	–	x	322.1	–9	–30.2
12	Gaussian	3	x	–	–	x	–	x	x	322.6	–15	–35.7
13	Gaussian	3	x	x	–	x	–	x	x	357.4	–16	–1.9
14	Gaussian	3	x	–	x	x	–	x	x	332.2	–17	–28.1
15	Gaussian	3	x	–	–	x	x	x	x	344.3	–21	–20.0

Note: The baseline model is the most expanded model presented in the text with $q = 3$ Gaussian components. x, constrained; –, not constrained.

Table 8. Parameter estimates at the stream level (Neste d'Oueil) and section level [Cires ($h = 1$), Mayrègne ($h = 2$), and Saint-Paul ($h = 3$)] by using model alternative 12 (Table 7).

Parameter	$q_{2.5\%}$	Estimate	$q_{97.5\%}$
10^3a	3.9	7.7	11.5
b	0.17	0.59	1.03
π_λ	0.3	9.6	37.6
π_μ	1.8	22.3	76.3
σ_1	6.5	7.1	7.7
σ_2	12.2	14.1	16.5
σ_3	28.2	40.0	48.7
τ_1	0.43	0.46	0.49
τ_2	0.23	0.29	0.36
τ_3	0.18	0.25	0.32
biom	13.95	15.47	17.07
λ	0.31	0.83	1.50
μ_1	43.1	52.8	61.9
μ_2	115.4	120.4	125.4
μ_3	159.1	174.5	194.3
biom_1	9.68	11.50	13.58
λ_1	0.46	0.53	0.59
$\mu_{1,1}$	45.6	47.2	48.7
$\mu_{1,2}$	117.6	121	124.3
$\mu_{1,3}$	160.5	176.6	195.7
biom_2	17.22	19.88	22.71
λ_2	0.90	0.98	1.07
$\mu_{2,1}$	51.4	52.4	53.3
$\mu_{2,2}$	117.6	120.3	123.0
$\mu_{2,3}$	155.0	169.8	192.3
biom_3	12.69	14.76	17.31
λ_3	0.56	0.62	0.69
$\mu_{3,1}$	57.9	59.0	60.2
$\mu_{3,2}$	115.8	119.5	123.3
$\mu_{3,3}$	161.1	177.0	193.7

dom spatial variability of the abundance, random spatial variability of the catchability, and residual variability of the catchability with fish. By using an index of complexity of fit, Laplanche (2010) suggested that a reduction with no variability of the catchability (among stream sections and residual) should be preferred. We have attained similar conclusions ($a_h = a$, $b_h = b$, and $1/\eta = 0$). Results show, however, that heterogeneity of the catchability between individuals is significant, and would be explained by heterogeneity of the catchability due to fish length. Once heterogeneity of the catchability due to fish length is accounted for, we find no significant decrease of the catchability across removals due to (residual) between individual variability of the catchability. Such a result does not hold the possibility of different sources of alteration of the catchability across removals, e.g., owing to adjustments of the behavior of the fish or of the electrofisher to depletion (Mahon 1980; Schnute 1983; Peterson et al. 2004). The extension of the current model together with model selection could help in evaluating the value of the consideration of additional sources of variability of the catchability.

Model selection suggests that variability between stream sections of the abundances (λ_h), the component centers ($\mu_{h,k}$), and the allometric parameters (c_h and (or) d_h) are significant. Biomass estimates are at Cires, Mayrègne, and Saint-Paul: 11.50 (9.68, 13.58), 19.88 (17.22, 22.71), and 14.76 (12.69, 17.31) g/m^2, respectively. Differences of total abundance (Bayley and Dowling 1993), growth (Ebersole et al. 2009), and as a result biomass (Bowlby and Roff 1986) are likely due to habitat variability. We believe that extending the current model by relating the above variables to key physico-chemical habitat covariates is an interesting perspective. This issue is discussed more thoroughly later by introducing several extensions of the current model.

The modeling of the length–abundance relationship as a mixture of Gaussian distributions may be inappropriate since the Gaussian probability density function is defined for all lengths. In this case study, expected population sizes for negative or large (>300 mm) length values are negligible. The use of a Gaussian kernel might be in that case satisfactory. We have also investigated the use of bounded, bell-shaped kernels. The comparison of model fit by using such a kernel (e.g., triweight) and the Gaussian kernel also suggests that the Gaussian kernel is acceptable. The use of a Gaussian kernel may, however, be problematic when mixing components of large variance. The use of different kernels has been suggested, for instance gamma kernels (Pitcher 2002). The current model can accustom any kernel given that it is possible to provide to WinBUGS a closed form of the probability density function of the kernel. We do not believe, however, that using a non-Gaussian kernel is the most promising solution to handle this issue. We rather suggest two different approaches. The first would be to extend the current model by constraining the component bandwiths to the centers, e.g., bandwiths proportionnal to centers. A second approach would be to separate components of large bandwiths into cohorts (of lesser bandwidths) by extending the current model with a growth submodel (which is discussed more thoroughly later).

The length–abundance plots of the catch at the Neste d'Oueil suggest that the use of three components would be satisfactory. Model comparison suggests that, indeed, a description of the abundance as a mixture of three components is fine. In this case study, the two first components unambiguously represent cohorts (0+ and 1+). The third component is not a cohort (brown trout in the Neste d'Oueil living longer than 3 years) but the mixture of several cohorts (2+ and older). Index of fit alone (deviance) suggests that the uses of three or four cohorts are comparable, index of complexity and fit (DIC) suggests that the use of three cohorts is preferable, prior knowledge suggests that the use of four or more cohorts is more realistic. One approach could be to set the number (q) and the definition sets of the centers (μ_c^{len}) of the cohorts by using prior knowledge and not use an index of complexity and fit. Another approach could be (once again) to extend the current model with a growth submodel and let the model separate the cohorts.

The error resulting on biom$_h$ of approximating fish weights $W_{h,l,f}$ by expectations $c_h L_l^{d_h} \exp(s_h^2/2)$ is negligible (as demonstrated in Appendix A). This holds if the population sizes n_h are sufficiently large. With lower population sizes, the consequences of the above approximation on the biomass estimate should be considered more closely. For that purpose, we suggest two solutions. The first option is to include the fish level within the biomass submodel and simulate the fish weights $W_{h,l,f}$ instead of the expected fish weights $E_f(W_{h,l,f})$ to compute biom$_{h,l}$. As a result, the posterior distribution of the biomass variables (hence interval estimates) takes into account inter-individual variability of the weight. The second option is to use an a posteriori Monte Carlo run: (*i*) run the model to compute an estimate of $\lambda_{h,l}$, (*ii*) simulate $n_{h,l}$, (*iii*) compute biom$_{h,l}$ by using eq. 9, simulate the fish weights $W_{h,l,f}$, and compute biom$_{h,l}$ by using eq. 8, (*iv*) compute both alternatives of biom$_h$ by using eq. 10 and their difference Δbiom$_h$, (*v*) repeat steps (*ii*–*iv*), (*vi*) estimate the standard deviations of Δbiom$_h$ ($h \in \{1, \ldots, s\}$). By using the dataset collected in the field, we find that the standard deviations of the error on biom$_1$, biom$_2$, and biom$_3$ by approximating the fish weights $W_{h,l,f}$ by the expectations $c_h L_l^{d_h} \exp(s_h^2/2)$ are 0.09, 0.10, and 0.10 g/m^2, respectively.

We have assigned vague priors to all free parameters. Laplanche (2010) conducted an informal sensitivity analysis to evaluate the consequences of different selections of vague priors. The author showed, in his case study, that only estimates at the stream level are sensitive to the choices of vague priors. The reason is that the author considered (as we have done here) a hierarchical structure to model the variability between three stream sections. The amount of information to provide estimates of parameters at the stream level is limited. By extrapolating his results, in the case that only interpretation of the data is inquired with minimum influence of prior knowledge, we would advise to use the abundance submodel with vague priors and report parameter estimates at the section level. In the aim of providing estimates at the stream level with minimum influence of prior knowledge, a larger number of sampling sections would be required. In the prospect of using prior knowledge, we provide the (approximate) parametrized marginal posteriors of the free parameters of the baseline abundance submodel. Marginal posterior parameters that are reported are specific to this case study. We could use the marginal posteriors reported as priors to further study the Neste d'Oueil, by using data collected in July of another year, for instance. One could also adjust the parametrization of the posterior distributions reported with expert knowledge to provide priors to a different study area.

In the aim of using the approach presented by Marin et al. (2005) to model abundance as a distribution mixture, we first regarded fish length as a continuous variable. On the other hand, to allow for random localization of the fish within a stream section (eq. 4), to incorporate the removal sampling model (eq. 1), and to compute biomass, we needed to consider fish length as a discrete variable. By regrouping fish within Δ_l = 1 mm length classes (equal to our measurement accuracy of the fish length), we could attain both objectives. In view of the computation time required to simulate the model with a Δ_l = 1 mm length class, we adapted the model to consider larger class widths. Regrouping fish counts within larger length classes results, however, in a loss of information. Using smaller class widths increases the number of measured variables but the complexity of the parametrization of the distribution mixture (3q per stream section) remains unchanged. In other words, using larger class widths does not make the distribution mixture model less complex and consequently more robust. Nevertheless, as reported, in the case of the simulated dataset, point and interval estimates of the parameters are not sensitive to the choice of the width of the length classes, given that the width is small enough. The reason is that when using datasets with large catches, the relative loss of information by grouping catches within larger size classes is negligible. With poorer datasets, the relative loss of information by grouping may not be negligible. Grouping catch within larger size classes also diminishes the capability of the model to detect variability of the catchability with length. By grouping, the amount of variation in catchability to be explained by length is reduced (since the amount of variation to be explained by length within a size class is null), consequently inflating the residual variability $1/\eta$. For such reasons, we recommend the use of a minimal class width when possible. With large datasets, grouping within larger size classes is conceivable.

We highlight some extensions to the current abundance-biomass model. One could relate parameters at the section level, either connected to catchability (η_h, a_h, b_h) or abundance (λ_h, $\tau_{h,k}$, $\mu_{h,k}$, $\sigma_{h,k}$), to environmental variables. With an appreciable number of sampling sections, parameters could be empirically related to habitat covariates (Rivot et al. 2008; Ebersole et al. 2009). Observations could be taken as independent, or parameters could be spatially related by using an auto-correlation model (Webster et al. 2008) completed by a Geographic Information System (Wyatt 2003). Higher hierarchical levels could be incorporated into the model to deal with a structured sampling strategy, like a larger spatial scale (e.g., watershed) or by integrating a time scale as done by Rivot et al. (2008). We believe that connecting the parameters of the distribution mixture through the development of a discrete population dynamics submodel and a growth submodel are interesting perspectives. The advantage of extending the abundance submodel with population dynamics and growth submodels is to derive variables (such as mortality, recruitment, and growth rates) more indicative of fish populations than component mixture parameters. The extensions suggested earlier (the use of environmental covariates, GIS, structured sampling) would in that case apply to the newly derived variables. As an illustration, we have extended the current abundance submodel with a growth submodel by relating growth rate and time of emergence to water temperature. An expanded hierarchical model would provide a unified framework where interval estimates of several variables indicative of fish populations (abundance, biomass, growth, mortality, recruitment, production, overweight, etc.) at a large spatial scale could be computed and used to study the biological health of freshwater sytems.

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Appendix A

The weight of a fish of length class *i* in section *h* is lognormally distributed of expectation $E_f(W_{h,i,f}) = c_h L_i^{d_h} \exp(s_h^2/2)$ and variance $\mathrm{var}_f(W_{h,i,f}) = (c_h L_i^{d_h})^2 \exp(s_h^2)[\exp(s_h^2) - 1]$. By using central limit theorem, the variables $\mathrm{biom}_{h,i}$ are approximately normally distributed of expectation $n_{h,i}E_f(W_{h,i,f})/A_h$ and variance $n_{h,i}\mathrm{var}_f(W_{h,i,f})/A_h^2$. Since the $\mathrm{biom}_{h,i}$ are independent, the biomass $\mathrm{biom}_h = \sum_{i=1}^{m} \mathrm{biom}_{h,i}$ of fish in section *h* is approximately normally distributed of expectation $\sum_{i=1}^{m} n_{h,i}E_f(W_{h,i,f})/A_h$ and variance $\sum_{i=1}^{m} n_{h,i}\mathrm{var}_f(W_{h,i,f})/A_h^2$. With $n_h = \sum_{i=1}^{m} n_{h,i}$ sufficiently large, the coefficient of variation of biom_h is approximately null.

The effect of sea lice (*Lepeophtheirus salmonis*) on juvenile pink salmon (*Oncorhynchus gorbuscha*) swimming endurance

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Abstract: The swimming endurance of naturally and experimentally infected juvenile pink salmon (*Oncorhynchus gorbuscha*) was measured to determine the effects of sea lice (*Lepeophtheirus salmonis*). Salmon naturally infected with adult male and preadult stage lice did not appear to have a reduced swim performance, but when experimentally infected with adult female lice, juvenile salmon showed a reduced ability to swim compared with uninfected control fish, and this effect increased with lice load. A reduced swimming endurance is not only likely to influence predation risk for salmon, but may have other ecological implications, such as slower seaward migration.

Résumé : Nous avons mesuré l'endurance à la nage de jeunes saumons roses (*Oncorhynchus gorbuscha*) infectés naturellement et expérimentalement pour mesurer les effets des poux de mer (*Lepeophtheirus salmonis*). Les saumons infectés naturellement avec des stades adultes mâles et pré-adultes des poux ne semblent pas avoir une performance de nage réduite; par contre, une fois infectés expérimentalement avec des poux adultes femelles, les jeunes saumons affichent une capacité de nage réduite par comparaison aux poissons témoins non infectés et l'effet augmente en fonction de la charge de poux. Une endurance réduite à la nage risque non seulement d'affecter la probabilité de prédation chez les saumons, mais peut avoir d'autres conséquences écologiques, telles qu'une migration plus lente vers la mer.

[Traduit par la Rédaction]

Introduction

Parasites play an important role in the ecology and survival of their hosts and can affect the behaviour and abilities of their hosts to carry out their day-to-day activities. For example, if the parasites create an energy drain on the host, less energy may be available for locomotion, especially costly movements (e.g., foraging forays, migration, escaping predators; Barber et al. 2000; Münderle et al. 2004; Östlund-Nilsson et al. 2005). Hosts may attempt to mitigate this energy deficit by altering their behaviour to increase energy intake or reduce activity, which can increase their susceptibility to predation (Lima and Dill 1990).

Although many parasites are relatively benign, situations may occur where these same parasites reduce host condition to the point of death (e.g., if abnormally abundant or infecting juveniles). High numbers of ectoparasitic sea lice (*Lepeophtheirus salmonis*) have been reported on out-migrating juvenile salmon in areas near fish farms in the Broughton Archipelago, British Columbia, and these have been suggested to cause up to 95% mortality (Morton et al. 2004, 2005; Krkošek et al. 2006). This study system provides an unparalleled opportunity to look at the potentially negative effects of a "novel" parasite (sensu Krkošek et al. 2007) on its host.

Many studies have examined the costs of *L. salmonis* infection to salmonid hosts (Pike and Wadsworth 1999; Tully and Nolan 2002; Wagner et al. 2008). For example, physiological damage and death in Atlantic salmon (*Salmo salar*) postsmolts was associated with infections by motile stage sea lice (Grimnes and Jakobsen 1996). Sustained swimming tests on adult *S. salar* found reduced swimming ability due to decreased cardiac output after exercise when infected with *L. salmonis* at 0.13 lice·g^{-1} (Wagner et al. 2003). Webster et al. (2007) found that infected juvenile pink salmon (*Oncorhynchus gorbuscha*) prefer fresh water and incur higher energy costs when in salt water, suggesting there are osmotic challenges associated with *L. salmonis* infection. Similarly, Wagner et al. (2004) found that adult Atlantic salmon performed better in freshwater than in saltwater swimming tests. Some studies used Fulton's condition factor to assess the effects of lice on juvenile pink salmon but found no difference in the condition factor of infected and noninfected fish (Jones and Nemec 2004; Butterworth et al. 2008). However, Morton and Routledge (2006, 2008) argue that condition factor is not a valid assessment of the impact

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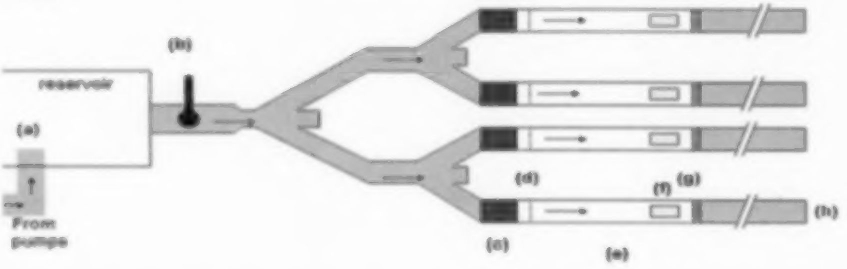
Fig. 1. Schematic drawing of swim tunnel seen from above. Water from pumps discharges into a 760 L plastic reservoir (*a*). Components are as follows: butterfly valve on 10.2 cm diameter polyvinyl chloride (PVC) pipe that is then reduced to 7.6 cm and split by Y-fittings (*b*), bundle of flow-straightening plastic drinking straws (*c*), 4 mm mesh screen (*d*), 7.6 cm × 76.2 cm clear PVC swim chambers (*e*), lid (*f*), electrified grid made of 0.5 mm diameter stainless steel wire mounted in a gate valve and connected to a variable transformer set to 2V AC (*g*), and outflow (*h*).



of sea lice on juvenile salmon, as their data suggest that condition factor is only reduced when the fish are moribund. Aside from the use (or misuse) of condition factor, there has not been any direct test of the effects of *L. salmonis* on juvenile pink salmon performance.

A prolonged swimming test was used to assess the impact of sea lice on the swimming endurance of naturally and experimentally infected salmon. Prolonged swimming tests, defined as high intensity swimming that lasts between 20 s and 120 min and ends in fatigue, are widely used to assess swimming performance (Beamish 1978; Hammer 1995). By measuring the point at which failure occurred, we tested the hypothesis that *L. salmonis* infection reduces juvenile pink salmon swimming endurance.

Materials and methods

Fish collection and maintenance

Natural infections

Wild juvenile pink salmon naturally infected with lice were collected with a beach seine (30.5 m × 2.5 m; 4 mm mesh) near Twin Lagoon, Broughton Archipelago, British Columbia. To be used in the experiment, all fish had to have a fork length of 53–57 mm, noninfected fish had to have zero lice (of any species) and no visual scarring (from either previous lice infections or predators), and infected fish had to have at least one motile *L. salmonis*, a chalimus scar (evidence of infection history), no other lice species, and no predator scars. Fish were visually assessed as in Krkošek et al. (2005), transferred to the Salmon Coast Research Station (Simoom Sound, British Columbia) in individual containers, and held overnight.

Experimental infections

Fish used in experimental infection trials were collected by seining in Spring Passage Channel and selected according to the same criteria as the noninfected fish above. Infected fish were held separately from test fish in flow-through floating tubs. Infection of previously noninfected fish with adult female lice gently removed from the infected fish occurred the following day.

Noninfected fish were selected haphazardly from holding tubs and placed into two buckets, randomly assigned as treatment or control groups. Treatment groups were manually infected with one, two, three, or four adult female lice, and the control group (no lice) was "sham infected" (i.e., all handling was the same except the placement of lice) at the same time. The fish to be infected was held in a small container partially filled with water, such that its dorsum was exposed; the louse was then manually placed on the fish. Because fish movement stimulated attachment, and to control for possible effects of anaesthetic on lice, fish were not anesthetized. Infections generally took less than 5 min, and fish were not out of water for more than 30 s. Handling times were kept consistent across treatment groups to ensure any difference between treatment levels were not due to increased emersion by repeating the procedure up to four times.

Swim tunnel design

Swim trials were conducted either the day following capture (naturally infected salmon) or approximately 38–46 h after experimental infection in a swim tunnel comprising four parallel chambers (Fig. 1). Fish were placed in the chambers through lids that sealed with a foam gasket and were secured by hose clamps. Stainless steel grids (mounted in gate valve housings in the rear of each swim chamber, allowing them to be raised to allow fish removal) remained electrified during trials but were switched off when the fish reached the endpoint (fatigue). The slight electrical current motivated the fish to continue swimming until complete exhaustion rather than resting against the grid. Water velocity in the chambers was regulated by adjusting the height differential between the water level in the reservoir and the outflow pipe; an adjustable overflow in the reservoir's side allowed excess water to spill once the desired height differential was achieved. These levels were calibrated to specific flow velocities by measuring flow volume over time.

Test protocol

Prior to each trial the reservoir and swim tunnel were flushed and filled with seawater. Four fish were chosen for each trial (when possible, two control and two treatment fish), placed randomly in a chamber and allowed to acclimate with no flow for 5 min. The swimming test was a constant acceleration test modified from Tierney et al. (2007), whereby water velocity was gradually increased to the initial velocity of 8.25 cm·s^{-1} over 1 min and then increased by 2.75 cm·s^{-1} every 5 min thereafter until the fish failed to

Table 1. Swimming and associated data for naturally and experimentally infected juvenile pink salmon.

				N					
Infection trial	Group	L_F (mm)	SD	Infected	Survived to testing	Failed	Censored	Median dmax (m)	Median motscr
Natural	NL	55.3	1.3	NA	42	27	15	719.56	NA
	L	54.9	1.3	NA	42	32	10	676.66	NA
Experimental	0	54.9	1.3	17	17	13	4	753.17	0
	1	54.9	0.9	14	13	12	1	590.70	2
	2	54.3	1.2	14	12	12	0	573.02	10
	3	55.4	1.6	16	9	8	1	439.89	12
	4	53.7	0.6	16	3	3	0	169.29	19

Note: Naturally infected fish (N = 84) were grouped by lice infection: no motile lice (NL) or motile lice (L). Experimentally infected fish (N = 54) were grouped by number of adult females (0–4). Juvenile pink salmon were experimentally infected for 40 h before testing. Censored data are the number of fish that did not fail. Median dmax is the distance at which 50% of fish failed, and motscr is the number of motile scars on juvenile pink salmon, counted after the trial. L_F, fork length; SD, standard deviation; NA, not applicable.

Table 2. Models representing competing hypotheses tested.

Model	Hypothesis
1. Lice + fork length + chamber	Lice effect
2. Lice + fork length + chamber + lice × fork length	Lice effect
3. Fork length + chamber	No lice effect
4. Null	No lice effect

Note: For experimentally infected juvenile pink salmon, lice = the number of adult females (0–4); for naturally infected fish, lice = infected or noninfected group.

continue swimming against the flow and remained against the grid for >2 s. Because maximum velocity attainable (37.75 $cm \cdot s^{-1}$) was reached before some fish failed, the final stage was extended an additional 30 min in those cases. Once the endpoint was reached, the grid was switched off for that chamber. At the end of the trial, all fish were flushed from the chambers into a net. Uninfected fish were later released near their collection point. Infected ones were sedated (clove oil) and euthanized so that motile louse scars could be counted as an indicator of lice damage. All protocols used in this research were approved by the Simon Fraser University Animal Care Committee (protocol #750B-05).

Eighty-four naturally infected fish (mean ± standard deviation (SD) fork length = 55.1 ± 1.3 mm) were swum between 15 and 27 May 2007. Trials on experimentally infected fish (n = 37) and their uninfected controls (n = 18) were performed between 6 and 21 June 2007 (see Table 1 for fork lengths). Water temperature was 8.6 ± 0.2 °C and salinity was 28–32 ppt in both sets of trials.

Analysis

Critical swimming speed calculations could not always be performed because the final stage sometimes had a longer duration and some fish did not fail. Therefore, cumulative distance swum (dmax) was calculated for each fish as an ecologically relevant measure of performance: the time (s) swum at each stage multiplied by the stage velocity and summed for all stages swum. Time to event (survival) analysis was used to quantify the effect of lice infection on fish performance because both data sets (naturally and experimentally infected fish) included censored data (31% and 11%, respectively). Fish that did not fail before the trial was ended were assigned an "at least distance swum" without failure and were considered as censored data. Kaplan–Meier (KM) estimates of the probability of swimming a given distance were obtained using observed dmax values. Parametric survival models (Table 2) representing competing hypotheses were fit to the KM survival estimates by log-likelihood using three different error distributions, for a total of 12 models. All models (excluding the null) included the main effects of fork length and chamber to account for any effects of fish size and consistent velocity variation between chambers. Models testing for an effect of lice included a lice variable: presence or absence of lice for naturally infected fish and number of adult female lice for experimentally infected fish. The number of motile scars was not included in the models as it was highly correlated with number of lice present.

Akaike's information criterion corrected for small sample sizes (AIC_c) was used to rank candidate models based on the relative differences (ΔAIC_c) between the model with the lowest AIC_c value and all other models in each set. AIC_c model weights (w; the probability that a given model is truly "best" among the candidate models) were also calculated. Because all models contribute some information and there is uncertainty about which is actually "best", all model w values were used to calculate estimated parameter likelihoods (importance of variable) and values, along with their unconditional standard error (SE). Only parameters with values ±2 SE that did not encompass zero were considered to have an effect (Burnham and Anderson 2002). All analyses were performed in R version 2.6.1 (R Development Core Team 2007).

Results

Natural infections

Fish in the naturally infected group (N_{NI} = 42) had a mean (± SD) of 1.31 ± 0.60 motile lice, but a majority were preadult stages and adult males (Fig. 2). Some salmon were also infected with other juvenile stages of lice. Median distances swum (i.e., the distance at which 50% failed) were 676.7 and 719.6 m for infected and noninfected salmon, respectively (Table 1; Fig. 3). Despite this 6% difference, the null model with a lognormal distribution was eight times more

Fig. 2. Numbers of *Lepeophtheirus salmonis* stages on the naturally infected juvenile pink salmon ($N = 42$) used in this study. Lice stages are as follows: copepodid (CP), chalimus 1 and 2 (CalA), chalimus 3 and 4 (CalB), preadult 1 and 2 male (PAM), preadult 1 and 2 female (PAF), adult male (AM), and adult female (AF).

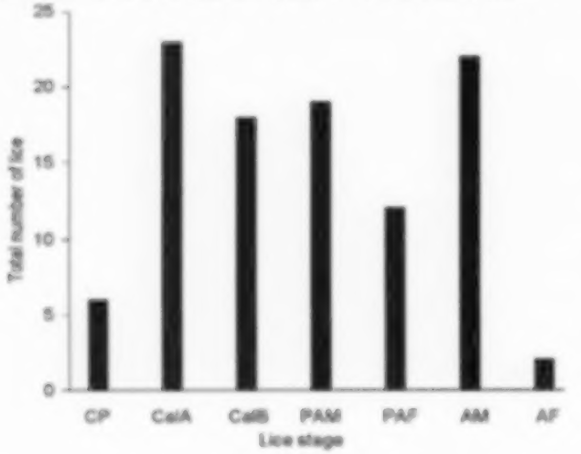


Fig. 3. Kaplan–Meier plot of the proportion of uninfected and naturally infected juvenile pink salmon still swimming after having swum a given distance. Each step indicates the distance where a swim failure event occurred; a plus symbol (+) indicates censored data (fish did not fail).

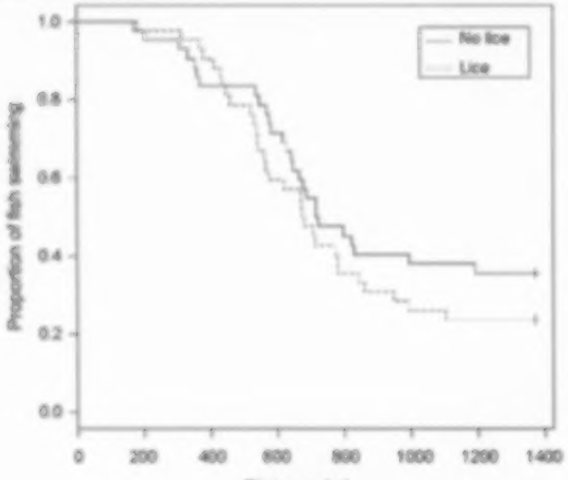
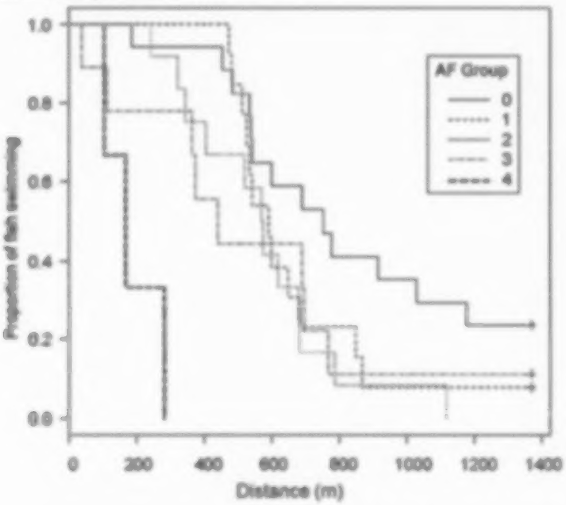


Fig. 4. Kaplan–Meier plot of the proportion of experimentally infected juvenile pink salmon still swimming after having swum a given distance. Each step indicates the distance where a swim failure event occurred; a plus symbol (+) indicates censored data (fish did not fail). Adult female (AF) group refers to the number of adult female lice per fish.



likely than the models incorporating an effect of lice to be the "best" model. Because of the superiority of the null model, no parameter estimates were calculated. These results suggest juvenile pink salmon swimming endurance is not reduced by natural infections of *L. salmonis* at the levels tested here.

Experimental infections

A total of 37 fish infected with 1, 2, 3, or 4 lice and 18 control fish were swum in this experiment (Table 1). The median distances infected salmon could swim before they failed were less than that for control fish (Table 1), and as the number of adult female (AF) lice increased, the distances fish could swim declined in a continuous fashion (Table 1; Fig. 4). The top ranking models included lice and fork length (L_{F})–AF interactions with a lognormal or Weibull error distribution and were two to three orders of magnitude more informative than the competing models (Table 3). The number of AFs had a large and significant negative effect on swimming endurance (Table 4). The interaction of L_{F} and AF had a significant positive effect on endurance, which can be interpreted as female lice having less of an effect on larger fish. Lice damage, as indicated by the number of motile scars, was highly correlated with the number of AF lice (Table 1; Spearman's rho = 0.815, $P < 0.01$).

Discussion

When experimentally infected with adult female lice, juvenile pink salmon had reduced swimming endurance. This seems biologically reasonable, given the large size and energy needs of the female parasites, which were acquiring resources to produce eggs (supported by evidence of females having fed on the test fish, i.e., motile scars). While there was a large overall effect of lice load, it was most evident for higher lice loads, particularly given that the majority of these fish died before they could be tested. Since only fish capable of withstanding the challenge of three and four lice were swum, the estimated impact of adult female lice on swimming endurance must be considered a conservative one. Although the maximum loads are high, the results are ecologically relevant, as loads of these magnitudes are found on naturally infected fish (Morton et al. 2004; Krkošek et al. 2006). Our findings are similar to those from the swimming tests performed by Wagner et al. (2003) on large Atlantic

Table 3. Summary of models for experimentally infected juvenile pink salmon.

Model and variables	Distribution	K	LL	AIC_c	Δ	w
1.[a] Adult female + fork length + chamber + adult female × fork length	Weibull	7	–556.7	1127.40	0.00	0.80
2. Adult female + fork length + chamber + adult female × fork length	Lognormal	7	–558.1	1132.63	2.80	0.20

Note: Model is Log(dmax) = intercept + model variables + $\sigma \times e$, where σ is a scale parameter and e is an error term based on Weibull or lognormal distributions (exponential error distributions did not provide an adequate fit). For each model, $N = 54$, K = number of model parameters, LL = maximum log-likelihood estimate, AIC_c = Akaike's information criterion corrected for small sample size, Δ = the change in AIC_c between the model and the model with the lowest AIC_c, and w = Akaike weight (the likelihood of superiority over other models in the set). Only models with $w > 0.001$ are shown.

[a] The model with the lowest AIC_c.

Table 4. Model parameters for experimentally infected juvenile pink salmon, parameter likelihoods (importance of variables), and estimates with unconditional standard error (SE).

Parameter	Parameter likelihood	Parameter estimates	Unconditional SE
Intercept[a]	1.00	20.31	5.26
Adult female[a]	1.00	–11.17	2.43
Fork length	1.00	–0.16	0.09
Chamber	1.00	0.08	0.32
Adult female × fork length[a]	1.00	0.20	0.04
Σ	1.00	–0.75	0.76
E	1.00	0.42	NA

Note: Parameters were calculated using w of both experimental swimming models in Table 3; other models, not shown, have $w = 0$ and thus do not influence parameter estimates. Values are rounded to the nearest 0.01.

[a] Parameter for which estimates ±2 unconditional SEs do not overlap 0, and therefore are considered significant.

salmon and to those reported for other fish host–parasite systems; parasites reduce prolonged swimming ability in the European eel (*Anguilla anguilla*; Münderle et al. 2004), the cardinal fish (*Cheilodipterus quinquelineatus*; Östlund-Nilsson et al. 2005), and unfed Atlantic cod (*Gadus morhua*; Martinez et al. 2003, 2004).

A parasite-induced decline in swimming endurance suggests that lice infection is energetically costly to pink salmon. There are several possible reasons for this. For example, adult females feed on blood, and its removal can induce anaemia (Wagner and McKinley 2004). To obtain the blood meal, a louse punctures the skin (causing the motile scars), which likely increases the energy required to maintain osmotic homeostasis. Repairing this tissue damage and fighting off secondary infections from these wounds is an additional cost. Because lice infections cause an increase in energy requirements, they may lead to reduced swimming ability if fish cannot compensate for lost resources.

In contrast with the results for experimentally infected salmon, naturally infected salmon showed no diminution of endurance. There are at least two possible explanations for this inconsistency. First, males (preadult and adult) comprised 83% of the lice on these fish. *Lepeophtheirus salmonis* males are smaller than females and likely have lower energy requirements. Since they are seeking out mating opportunities, they may not feed as often or as much as females and thus may be less detrimental. Studies of the effects of sea lice on Atlantic (Dawson et al. 1999; Wagner et al. 2003; Wells et al. 2006) and Pacific (Morton and Routledge 2005; Krkošek et al. 2006) salmonids found that the onset of pathogenicity began with the preadult stages, but did not look at gender-specific effects.

A second possibility is that the current level of motile lice on a host fish is not a good indicator of past lice intensity on that fish or the duration of that infection and thus is only weakly correlated with the host's current swimming ability. To account for this, tests were performed on fish that had a chalimus scar as evidence of prior infection; however, given the transient nature of motile lice and the fact that juvenile pink salmon are able to rid themselves of lice (Jones et al. 2007; M. Krkošek, University of Washington, School of Fishery and Aquatic Sciences, Seattle, WA 98195, USA, personal communication, 2007), this may have been insufficient to account for their infection history. It would thus be premature to conclude that there is no effect of the lice stages represented on the naturally infected salmon, but rather that snapshot tests such as these are insufficient to determine effects on swimming ability. Future studies should use experimental infections or track infections over time.

Reduced swimming endurance could have ecological consequences for salmon. Because juvenile salmon migrate in large shoals, a fish with reduced swimming endurance may be less able to compete for food, maintain its position within the shoal, or remain with the shoal at all, thereby losing the benefits that the shoal provides, such as protection from predators. Reduced swimming endurance may also increase predation susceptibility if it makes infected individuals less likely to escape from a coursing predator, such as a coho salmon (*Oncorhynchus kisutch*) or cutthroat trout (*Oncorhynchus clarkii*). The costs incurred from infections may also increase infected salmon susceptibility to predation if, in an attempt to mitigate these costs, they increase their foraging effort and thus their exposure to predators (see Mages 2008).

This study is the first to use swimming tests on wild juvenile pink salmon performed in a field lab in close proximity (<5 km) to collection sites and demonstrates that experimental infection is essential when testing for the effects of lice on swimming performance and perhaps other measures of condition. As suggested by the two control groups having very similar median swimming distances, fish were not placed under additional stress because of the experimental infection methodology, suggesting that the infection protocol used in this study is a valid method with which to assess the effects of motile lice on fish swimming performance.

Overall, the findings illustrate the need for further work using swimming tests, both on fish naturally infected with varying (and higher) numbers of adult lice and on those experimentally infected, to investigate the effects of other lice stages and infection durations. These tests should be run concurrently with physiological measurements to understand the mechanisms underlying any effects observed. Information gained from such studies will shed light on the impact of *L. salmonis* infections on wild juvenile pink salmon. This is the first study to show an effect of sea lice on juvenile salmon swimming endurance, and while direct mortality may be an important driver of population declines, reductions in swimming performance may contribute to the impact of sea lice on pink salmon populations.

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DISCUSSION / DISCUSSION

Comment on “Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)”[1]

Jonathan B. Armstrong

Abstract: In their recent article, “Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)” (Can. J. Fish. Aquat. Sci. **66**(9): 1546–1553), Garner et al. observed salmon eggs in the stomach contents of mature Chinook, coho, and chum salmon. Through experimentation and simulation of salmon energetics, the authors conclude that the observed feeding represents an important gain in energy, challenging the accepted paradigm that assumes salmon energy budgets contain no gains once adults return to freshwater. Here, I argue that Garner et al. have overestimated the energetic consequence of egg consumption and that the observed consumption rates do not represent biologically significant gains in energy.

Résumé : Dans un article récent, « Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.) » (J. Can. Sci. Haleut. Aquat. **66**(9): 1546–1553), Garner et al. ont noté la présence d’œufs de saumons dans les contenus stomacaux de saumons chinook, coho et kéta matures. Par des expériences et des simulations de l’énergétique des saumons, les auteurs concluent que la consommation observée représente un gain important d’énergie, ce qui met en doute le paradigme accepté qui assume que les bilans énergétiques des saumons ne font aucun gain une fois les adultes retournés en eau douce. Je prétends ici que Garner et al. ont surestimé les conséquences énergétiques de la consommation d’œufs et que les taux de consommation observés ne représentent pas des gains en énergie biologiquement significatifs.

[Traduit par la Rédaction]

In many freshwater systems with fishable returns of Pacific salmon, one can find anglers attempting to lure these fish with salmon eggs or imitations thereof. In the recent publication, “Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.),” Garner et al. (2009) provide scientific documentation of what anglers have long known: adult salmon occasionally eat eggs. However, as many disappointed anglers can attest, Garner et al. found that egg consumption by adult salmon was generally rare. The authors explored the biological consequences of the observed levels of consumption through experimentation and simulation of salmon energetics, concluding that their results provide a “fundamental shift in our understanding of Pacific salmon ecology,” which previously assumed that energetic gains were negligible once adult salmon return to fresh water. Instead, Garner et al. claim that the energy from egg consumption helps salmon travel farther and survive longer during spawning migrations. While I find this work interesting and thought provoking, I challenge the authors’ claim that salmon feeding substantially alters the energy budgets of migrating salmon.

The energetic consequences of egg consumption are overstated by the authors’ analysis. The energy density assumed for salmon eggs, 18.7 $kJ \cdot g^{-1}$ wet mass, is roughly two times larger than reasonable estimates of this parameter. Garner et al. cite Meka and Margraf (2007), who did not actually measure this parameter, but reference an unpublished Master’s thesis (Eastman 1996), which also did not measure the parameter. While it is not clear how this estimate was derived, it is clearly inaccurate. Hendry and Berg (1999) researched salmon energetics in the same populations studied by Eastman and found a mean energy density of 7.8 $kJ \cdot g^{-1}$ wet mass for ripe eggs (standard deviation = 0.5). A survey of the literature reveals that this parameter varies from approximately 7 to 12 $kJ \cdot g^{-1}$ across different species of *Oncorhynchus* and *Salmo* (Table 1). Accordingly, Garner et al.’s estimate of the energy density of salmon eggs, and thus their conclusions regarding energetics consequences for egg predators, are exaggerated by about two times.

Regardless of the energy density of salmon eggs, it is not clear that Garner et al.’s observed consumption rates represent meaningful feeding or energetic gains. The average feeding rate Garner et al. observed in adult salmon was less than 1 $egg \cdot day^{-1}$. This value is decidedly low when placed into context with other fishes that exploit Pacific salmon eggs (Scheuerell et al. 2007; Denton et al. 2009; Armstrong et al. 2010). For instance, adult rainbow trout (*Oncorhynchus mykiss*) and Dolly Varden (*Salvelinus malma* are regularly found with hundreds of Pacific salmon eggs in their

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Table 1. Published estimates of egg energy density in trout and salmon.

Species	Energy density ($kJ \cdot g^{-1}$ wet mass)	Source
Atlantic salmon (*Salmo salar*)	8.5	Jonsson et al. 1997
Atlantic salmon	7.2 (0.5)	Berg et al. 2001
Brown trout, resident (*Salmo trutta*)	8.4 (0.4)	Jonsson and Jonsson 1997
Brown trout, anadromous	7.8 (0.5)	Jonsson and Jonsson 1997
Sockeye salmon (*Oncorhynchus nerka*)	10.8[a]	Crossin et al. 2004
Sockeye salmon	7.8 (0.5)	Hendry and Berg 1999
Sockeye salmon	8.5	Hendry et al. 2000
Chinook salmon (*Oncorhynchus tshawytscha*)	11.1 (0.1)	Mesa and Magie 2006
Pink salmon (*Oncorhynchus gorbuscha*)	11.2	Crossin et al. 2003

Note: The values shown here are the mean energy density of ripe eggs sampled prior to the completion of spawning. The standard deviation, if reported, is shown in parentheses.

[a] Crossin et al. (2004) reported data as a range. The midpoint of this range is shown here.

Fig. 1. A photograph of a Dolly Varden (*Salvelinus malma*) and hundreds of sockeye salmon (*Oncorhynchus nerka*) eggs that comprised its stomach contents. Salmonids that actively feed on Pacific salmon eggs achieve much higher rations than Garner et al. observed in mature Pacific salmon. (Photo courtesy of Thomas P. Quinn, Alaska Salmon Program, University of Washington, Seattle, Washington.)

stomachs (Fig. 1) (Denton 2008; T.A. Jaecks, Alaska Department of Fish and Game, Sport fish Division, 546 Kenny Wren Road, Dillingham, Alaska, unpublished data). In contrast, the highest ration reported by Garner et al. was 14 eggs·day^{-1} and appears to occur infrequently, as 87% of the salmon surveyed did not have eggs in their stomach. The authors suggest that these small rations are biologically meaningful because the fish in their experiments consumed a similar number of eggs per day and were able to maintain their body mass (losses < 0.03% body mass·day^{-1}). However, the fish in the authors' feeding experiment weighed 1/7 as much as the fish they sampled in the wild (mean mass = 565 and 4200 g, respectively), so the mass-specific rations of observed and experimental fish were not similar. In fact, bioenergetics analysis (Hanson et al. 1997) suggests the authors' maximum observed feeding rate (14 eggs·day^{-1}) was less than 1/4 of the ration required for a 4200 g coho salmon (*Oncorhynchus kisutch*) to maintain body mass (68 eggs·day^{-1} in 7.5 °C water). While the authors' experimental results convincingly suggest that adult salmon can digest and metabolize eggs, they do not suggest that the low rations observed in wild adult salmon were biologically significant.

Using the average feeding rate observed by Garner et al. (1 egg·day^{-1}) and an energy density for salmon eggs of 9 $kJ \cdot g^{-1}$, the average adult salmon consumed only 2.4 kJ·day^{-1}, producing 1.6 kJ·day^{-1} of available energy (accounting for indigestible portions and egestion according to Garner et al.). Following the energetics approximations used by Garner et al., a 5 kg salmon feeding at the average observed rate would gain an additional 3 min of survival per day on the spawning grounds. Feeding activity itself likely increases energetic costs, increases predation risk, and decreases the ability to find and defend mating sites. The egg consumption observed by Garner et al. is unlikely to increase energy or fitness in biologically significant ways and actually reinforces the assumption that salmon, in effect, stop feeding upon reaching freshwater.

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DISCUSSION / DISCUSSION

The importance of freshwater feeding in mature Pacific salmon: a reply to the comment by Armstrong on "Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)"[1]

Shawn R. Garner, John W. Heath, and Bryan D. Neff

Abstract: Armstrong has questioned the biological relevance of the feeding observations that we presented in the study "Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.)" (Can. J. Fish. Aquat. Sci. **66**(9): 1546–1553). Here we discuss his arguments and show that feeding can provide substantial energetic gains, which would, for example, allow feeding salmon to maintain body condition for up to an additional 23 days. Many consequences of feeding by mature Pacific salmon remain to be explored, but our study shows that these fish do feed in fresh water and that the benefits can be substantial.

Résumé : Armstrong a remis en question la pertinence biologique des observations d'alimentation que nous avons présentées dans « Egg consumption in mature Pacific salmon (*Oncorhynchus* spp.) » (J. Can. Sci. Haleut. Aquat. **66**(9): 1546–1553). Nous examinons ses arguments et démontrons que l'alimentation peut fournir des apports énergétiques substantiels, qui pourraient, par exemple, permettre aux saumons qui s'alimentent de maintenir leur condition corporelle jusqu'à 23 jours supplémentaires. Il reste de nombreuses conséquences de l'alimentation par les saumons du Pacifiques matures à explorer, mais notre étude montre que ces poissons s'alimentent de fait en eau douce et que les bénéfices peuvent être importants.

[Traduit par la Rédaction]

Sport fishermen have long known that mature Pacific salmon (*Oncorhynchus* spp.) will strike at objects that resemble eggs (e.g., Rutter 1903). However, because of the deeply entrenched belief that mature Pacific salmon cease feeding in fresh water, a number of fanciful explanations have been put forward in popular folklore to explain this behaviour. Mature salmon have at times been postulated to strike at eggs as a maladaptive vestige of oceanic feeding behaviour or as a way to eliminate potential competitors that their offspring might encounter as juveniles. Our study supports a far simpler explanation for this behaviour: Pacific salmon continue to feed because it provides them with nourishment (Garner et al. 2009).

Armstrong (2010) presents several arguments challenging the interpretation of our data. First, the author questions the choice of parameters we used in our energetic simulations. Second, the author suggests that the feeding rates we observed were insignificant compared with rates observed in other salmonids that feed on eggs. Third, the author questions whether the energy obtained from consuming eggs is biologically relevant. Fourth, the author questions the profitability of a feeding strategy in mature salmon. Below we outline our response to these points.

First, after further investigation of the energetic content of salmon eggs reported in Meka and Margraf (2007), we agree with Armstrong that this value is high. Examination of the methods used to determine energetic content in salmon eggs, which were described by Wetzel (1993), showed that the sample storage conditions were likely the source of the inflated values. Regardless, as we detail below, our conclusions are not affected when we instead use the conservative value of 9 $kJ \cdot g^{-1}$ suggested by Armstrong (2010). Furthermore, our values represent minimum estimates because our calculations of feeding rates were conservative. For example, the dead fish that we collected in the rivers likely underestimated feeding rates because of both loss of appetite

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during senescence and declining availability of eggs late in the breeding season. The fish that we sampled at hatcheries had been held in the hatchery environment for an indeterminate length of time and may have had reduced feeding opportunities without access to breeding areas.

Second in the comment, Armstrong (2010) highlights that several other species of salmonids that feed on salmon eggs have considerably higher feeding rates than were observed in our study of Pacific salmon (e.g., Scheuerell et al. 2007; Denton et al. 2009; Armstrong et al. 2010). However, all of the studies Armstrong details focus on stream resident fishes that were not reproductively active and were thus able to devote their time entirely to foraging. The rations that we observed are in fact quite comparable to other migratory salmonids that feed opportunistically during migration and spawning. For example, two studies of mature sea-run brown trout (*Salmo trutta*) showed that about 25% of individuals continued to feed when they were in freshwater locations without access to marine prey (Harris 1971; Elliott 1997). In mature Atlantic salmon (*Salmo salar*), stomach contents showed that 30% of the fish continued to feed after returning to fresh water (Johansen 2001), whereas in white-spotted charr (*Salvelinus leucomaenis*), only 9% of the fish fed during upstream migration (Takami et al. 1996). Our finding of egg consumption by 13% of the Pacific salmon that we sampled is thus within the range of previously observed values in migratory salmon, while the 27% prevalence that we observed in Quinsam River coho salmon (*Oncorhynchus kisutch*) is in the upper end of that range. It is also interesting that all of the species we studied were semelparous, whereas the other studies on migratory salmon looked at iteroparous species, which suggests that reproductive strategy does not directly dictate feeding rates. While we do not contest that migratory salmon rely extensively on energy accumulated prior to migration to complete spawning, our study and these others on migratory salmonids clearly suggest that these fishes also use opportunistic feeding in fresh water to support the costs of migration and breeding.

Third, we argue that consuming eggs can provide mature Pacific salmon with biologically relevant amounts of energy. Of course, as pointed out by Armstrong (2010), an average fish in our study, which weighed about 5 kg and fed at a rate of 1 egg per day, would achieve only modest energetic gains. However, this calculation ignores the variation in our data, not to mention it includes populations where our data suggest that feeding was both uncommon and likely to be less important. If we examine the variation in our data more closely, our most actively feeding fish was a coho salmon jack that weighed only 0.37 kg and had 159 eggs in his stomach. Using the energetic model and parameters applied by Armstrong (from Hanson et al. 1997), the energy from the eggs present in this fish's stomach would be sufficient to sustain his body mass for more than 23 days. Moreover, 71% of the coho salmon jacks that we observed feeding consumed eggs at a rate that was more than double that needed to maintain their body mass (n = 7, body mass = 0.34–074 kg). The energetic gains associated with egg consumption in Pacific salmon may thus be particularly important for precocial males (also see Maekawa and Hino 1987; Blanchfield and Ridgway 1999). On the other hand, one of our most surprising findings was that large individuals were no less likely to feed than their smaller counterparts. Indeed, we observed the highest feeding prevalence in nonprecociously maturing female coho salmon from the Quinsam River, in which 40% of the sampled females had consumed eggs. Importantly, female salmon may continue to feed in fresh water not only to offset the relatively higher costs of breeding that they incur (Hendry and Berg 1999), but to obtain physiologically important resources, including carotenoids and dietary protein (Ketola 1982; Blount et al. 2000; Garner et al. 2010). Regardless of the exact benefits associated with consuming eggs, such feeding can offer biologically important benefits to mature Pacific salmon.

Fourth, Armstrong (2010) argued that the benefits of feeding would be outweighed by, for example, the energetic cost of feeding, increased exposure to predators, and interference with mating opportunities. Our behavioural observations instead suggest that individuals that consumed eggs on the breeding ground fed opportunistically and at low cost. Eggs were captured when suspended in the water column near where salmon were already defending a spawning territory. Feeding in this manner never required an individual to swim more than 3 m and would prevent mating only for a few seconds. In the case of individuals that we observed with large numbers of eggs in their stomachs (i.e., up to 159 eggs), they were instead using an intensive feeding strategy that may have incurred costs by both forgoing spawning opportunities and risking injury from larger fish defending their nests. However, for actively feeding individuals the costs of foraging could be balanced by substantial energetic gains such as the resources to maintain body condition for 23 days as we calculated above. We postulate that mature Pacific salmon adjust their foraging behaviour in response to their individual energetic state, which will ultimately determine the value of incurring the costs associated with an active feeding strategy.

Overall, we agree with Armstrong (2010) that many consequences of feeding behaviour for the breeding energetics of Pacific salmon remain to be explored. For example, we observed considerable differences in feeding behaviour among populations over even a small geographic scale, so it is still too early to make widespread generalizations about freshwater feeding patterns across systems. Nevertheless, our study fundamentally alters the understanding of the breeding ecology of Pacific salmon by shifting the burden of proof. Where once it was acceptable to dismiss freshwater feeding by mature Pacific salmon out of hand, there is surprisingly little data to support this belief. Our study instead shows that Pacific salmon do feed in fresh water and that the energetic and physiological benefits may be substantial.

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ERRATUM / ERRATUM

Erratum: Incorporating lakes within the river discontinuum: longitudinal changes in ecological characteristics in stream–lake networks

Nicholas E. Jones

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On page 1357 of the published article, the final sentence of the caption for Fig. 8 was truncated. The caption should read as follows:

Fig. 8. (*a*) Trellis and (*b*) dendritic network drainage patterns and respective basin shapes illustrate how basin shape influences lake effects. A single lake in the midreaches of a trellis network may alter the ecological characteristics (e.g., flow regime) without dilution from large neighbouring network branches for many kilometres. In contrast, the same placement of a lake in the dendritic basin will lead to ecological changes that are soon diluted by tributaries.

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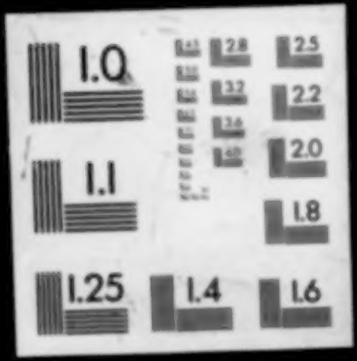
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